40315

National Library of Canada / Bibliothèque nationale du Canada

CANADIAN THESES ON MICROFICHE / THÈSES CANADIENNES SUR MICROFICHE

NAME OF AUTHOR/*NOM DE L'AUTEUR* JOSEPH WAI HUNG SO

TITLE OF THESIS/*TITRE DE LA THÈSE* A STUDY ON PREDATOR - PREY FOOD CHAINS

UNIVERSITY/*UNIVERSITÉ* UNIVERSITY OF ALBERTA

DEGREE FOR WHICH THESIS WAS PRESENTED/ *GRADE POUR LEQUEL CETTE THÈSE FUT PRÉSENTÉE* M SC

YEAR THIS DEGREE CONFERRED/*ANNÉE D'OBTENTION DE CE GRADE* 1978

NAME OF SUPERVISOR/*NOM DU DIRECTEUR DE THÈSE* DR H I FREEDMAN

Permission is hereby granted to the NATIONAL LIBRARY OF CANADA to microfilm this thesis and to lend or sell copies of the film.

The author reserves other publication rights, and neither the thesis nor extensive extracts from it may be printed or otherwise reproduced without the author's written permission.

L'autorisation est, par la présente, accordée à la BIBLIOTHÈQUE NATIONALE DU CANADA de microfilmer cette thèse et de prêter ou de vendre des exemplaires du film.

L'auteur se réserve les autres droits de publication; ni la thèse ni de longs extraits de celle-ci ne doivent être imprimés ou autrement reproduits sans l'autorisation écrite de l'auteur.

DATED/*DATÉ* Aug 16, 1978 SIGNED/*SIGNÉ* So Wai Hung

PERMANENT ADDRESS/*RÉSIDENCE FIXÉ* 10 Mok Cheong St., 5th floor,
To Kwa Wan, Kowloon, Hong Kong

NL-91 (3-74)

National Library of Canada

Cataloguing Branch
Canadian Theses Division

Ottawa, Canada
K1A 0N4

Bibliothèque nationale du Canada

Direction du catalogage
Division des thèses canadiennes

NOTICE

The quality of this microfiche is heavily dependent upon the quality of the original thesis submitted for microfilming. Every effort has been made to ensure the highest quality of reproduction possible.

If pages are missing, contact the university which granted the degree.

Some pages may have indistinct print especially if the original pages were typed with a poor typewriter ribbon or if the university sent us a poor photocopy.

Previously copyrighted materials (journal articles, published tests, etc.) are not filmed.

Reproduction in full or in part of this film is governed by the Canadian Copyright Act, R.S.C. 1970, c. C-30. Please read the authorization forms which accompany this thesis.

THIS DISSERTATION
HAS BEEN MICROFILMED
EXACTLY AS RECEIVED

AVIS

La qualité de cette microfiche dépend grandement de la qualité de la thèse soumise au microfilmage. Nous avons tout fait pour assurer une qualité supérieure de reproduction.

S'il manque des pages, veuillez communiquer avec l'université qui a conféré le grade.

La qualité d'impression de certaines pages peut laisser à désirer, surtout si les pages originales ont été dactylographiées à l'aide d'un ruban usé ou si l'université nous a fait parvenir une photocopie de mauvaise qualité.

Les documents qui font déjà l'objet d'un droit d'auteur (articles de revue, examens publiés, etc.) ne sont pas microfilmés.

La reproduction, même partielle, de ce microfilm est soumise à la Loi canadienne sur le droit d'auteur, SRC 1970, c. C-30. Veuillez prendre connaissance des formules d'autorisation qui accompagnent cette thèse.

LA THÈSE A ÉTÉ
MICROFILMÉE TELLE QUE
NOUS L'AVONS REÇUE

NL-339 (3/77)

THE UNIVERSITY OF ALBERTA

A STUDY ON PREDATOR-PREY FOOD CHAINS

by

JOSEPH WAI HUNG SO

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF MATHEMATICS

EDMONTON, ALBERTA

FALL, 1978

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled A STUDY ON PREDATOR-PREY FOOD CHAINS submitted by JOSEPH WAI HUNG SO in partial fulfilment of the requirements for the degree of Master of Science.

Dr. H. Freedman
(Supervisor)

G. J. Butler

Arthur J. Hales

Curtis Shirbeck

Date: Aug. 1/78.

To my parents

ABSTRACT

In view of the recent interest in mathematical models simulating food chains, the present dissertation is devoted to a study of some aspects of predator-prey food chains by means of deterministic mathematical models. These aspects include: boundedness of species numbers, stability of equilibria (both local and global), persistence and survivability, alternating equilibrium numbers phenomenon, perturbations (autonomous and periodic), effect of selection on the abundance of species, and, relationship between stability and complexity. My main results are Theorem 4.4.1 and Theorem 4.6.1. There I show that for Lotka-Volterra food chains of any length n with a carrying capacity in the first species, the positive equilibrium, if it exists, will automatically be globally stable. Hence there cannot be any non-trivial limit sets such as periodic orbits or recurrent motion. Moreover, if the parameters are varied in such a way as to make the positive equilibrium disappear, then at the instant of disappearance of this positive equilibrium it coincides with the equilibrium of one dimension lower, making the latter globally stable and so on.

ACKNOWLEDGEMENTS

I wish to express my deep gratitude to my supervisor, Dr. H. I. Freedman, for his guidance and invaluable assistance throughout this research, as it is he who introduced me to the subject of Mathematical Ecology. For this I am deeply grateful.

I would also like to thank all my friends in Canada for their warm acceptance of a foreigner, and especially Dr. G. J. Butler, who made some very useful comments, and Mr. J. A. Brooke, with whom conversation, mathematical or otherwise, is always simulating.

Finally, my thanks go to the University of Alberta and NRC Grant A 4823, of which Dr. H. I. Freedman is the principal investigator, for their financial support and to Miss June Talpash for her excellent typing.

TABLE OF CONTENTS

CHAPTER		Page
I	INTRODUCTION	1
	1.1 Background and Survey of Literature	1
	1.2 Mathematical Preliminaries	6
	1.3 Outline of Thesis	12
II	GENERAL FOOD CHAINS	13
	2.1 Assumptions	13
	2.2 A Stability Theorem	17
	2.3 General Theorems on Persistence and Survivability	22
III	INTERMEDIATE FOOD CHAINS	26
	3.1 Boundedness of Solutions	26
	3.2 Existence and Stability of Equilibrium Points for $n = 4$	30
IV	LOTKA-VOLTERRA FOOD CHAINS WITH OR WITHOUT CARRYING CAPACITY	49
	4.1 Introduction	49
	4.2 A Liapunov Function	51
	4.3 Persistence and Survivability	56
	4.4 Equilibria for (I_n)	66
	4.5 Alternating Equilibrium Numbers Phenomenon	75
	4.6 Global Stability	81
	4.7 Some Perturbation Theorems	93

CHAPTER		Page
V	EFFECT OF EVOLUTION ON EQUILIBRIUM NUMBERS . . .	97
	5.1 Introduction	97
	5.2 n = 3, 4	101
	5.3 General n	105
VI	SOME EXAMPLES	121
	6.1 Example 1	122
	6.2 Example 2	125
	6.3 Example 3	128
VII	SUMMARY AND DISCUSSION	131

***

BIBLIOGRAPHY 133

CHAPTER I

INTRODUCTION

§1.1 Background and Survey of Literature

Recently there has been considerable interest in mathematical models simulating predator-prey food chains. In the case of food chains of arbitrary length, the most general Kolmogorov-type model is looked at by Rescigno and Jones [1] who give some hypothesis and geometrical interpretation of the equilibrium leading to oscillatory phenomena. Saunders and Bazin [2] consider the stability and the effect of enrichment on the stability of a food chain in a chemostat using an intermediate-type model. More recently, Gard and Hallam [3] give sufficient conditions for the persistence and non-persistence of Lotka-Volterra type food chains. For food chains of length three, Rosenzweig [4] and Wollkind [5], using graphical methods, analyze the neighborhood stability of the possible equilibria of a general food chain model simulating the plant-herbivore-carnivore dynamics. Freedman and Waltman [6] examine the survivability of all species of an intermediate type model. Hausrath [7] considers a perturbed Lotka-Volterra type model in which the highest trophic level is not soley limited by the middle level and he shows the existence of a perturbed asymptotically stable equilibrium. More recently, Lin and Kahn [8] discuss the existence of a bifurcation of equilibria and calculate to the lowest approximation the periodic solution around one of the unstable equilibria of food chains having Lotka-Volterra type and Holling type of predation. Food chain models

where both biomass and energy have been taken into consideration can be found in May [9] and Hirata and Fukao [10].

All the food chain models considered by the above authors can be included in the following ecocommunity model of n variables (c.f., Levins [11]):

$$(1.1.1)\qquad \begin{cases} x_1' = f_1(x_1,x_2,\ldots,x_n;\ C_1,C_2,\ldots) \\ x_2' = f_2(x_1,x_2,\ldots,x_n;\ C_1,C_2,\ldots) \\ \cdots \\ x_n' = f_n(x_1,x_2,\ldots,x_n;\ C_1,C_2,\ldots) \end{cases}$$

where $' = \frac{d}{dt}$ and t denotes time.

That is, the growth rate of x_i is some function (called the growth function) f_i of all the variables $x_1,x_2,\ldots,x_n$ in the system and a set of parameters $C_1,C_2,\ldots$.

Here, for simplicity, we shall assume the variables x_i $(i = 1,2,\ldots,n)$ is the abundance (number or biomass) of the i^{th} species. Generally speaking, the variables can also represent the energy content of the species, the level of resources used by the species or some factor produced by a species such as a toxic by-product or a predation pressure. The parameters $C_1,C_2,\ldots$ are of several kinds. Some are environmental parameters beyond the influence of the species such as temperature, rainfall or vegetation density. Some depend on the genotype of a species, on such inheritable traits as its fecudity or heat tolerence. Still others are dependent on more than one species. For instance, the rate of predation of x_j on x_i depends on the biology of both.

By using (1.1.1) as our starting point, we have made the implicit assumption that the size of each population can be measured by real numbers, that no random fluctuations are present and that the age structure composition of the population is constant or irrelevant. (For a justification of using deterministic models such as (1.1.1), instead of the probably more realistic stochastic models, one may refer to Smith [12]).

Let $C_1, C_2, \ldots \in P$ (the parameter space of interest) be fixed. Then (1.1.1) becomes

$$(1.1.2) \qquad \begin{cases} x_1' = f_1(x_1, x_2, \ldots, x_n) \\ x_2' = f_2(x_1, x_2, \ldots, x_n) \\ \vdots \\ x_n' = f_n(x_1, x_2, \ldots, x_n) \end{cases}$$

We shall assume that

(i) $f_1, f_2, \ldots, f_n : R_+^n \to R$, where $R_+^n = \{x \in R^n : x_i \geq 0 \quad \forall 1 \leq i \leq n\}$, are continuous and sufficiently smooth to guarantee that the initial value problem for (1.1.2) with initial condition $\in R_+^n$ will have a unique solution. Note that we only require the solution to be defined on some interval $[0,T)$ where $T > 0$ may be $< \infty$. (Standard sufficiency theorems for existence and uniqueness are given in Coppel [13]).

(ii) The hyperplanes $H_i = \{x \in R_+^n : x_i = 0\} \quad (i = 1,2,\ldots,n)$ are invariant sets of (1.1.2).

This is true, for example, if (1.1.2) is of the form

$$
(1.1.3)\qquad \begin{cases} x_1' = x_1\, g_1(x_1,x_2,\ldots,x_n) \\ x_2' = x_2\, g_2(x_1,x_2,\ldots,x_n) \\ \cdot \\ \cdot \\ \cdot \\ x_n' = x_n\, g_n(x_1,x_2,\ldots,x_n) \end{cases}
$$

Clearly, this assumption is biologically reasonable.

Since the state space of ecological interest is the invariant set R_+^n instead of R^n, notions such as equilibrium points, stability, asymptotic stability, global stability, periodic solution, recurrent motion, etc. refer to solutions of (1.1.2) in R_+^n. Their mathematical definitions are given in Bhatia and Szego [14]. Discussion of some of these concepts within the ecological setting can be found in May [15] and Lewontin [16].

Following Gard and Hallam [3], (1.1.2) is said to be <u>persistent</u> if each solution $x(t)$ of (1.1.2) with

$$x(0) \in \mathrm{Int}(R_+^n) = \{x \in R_+^n : x_i > 0 \quad \forall 1 \le i \le n\}$$

satisfies

$$(1.1.4)\qquad \overline{\lim_{t \to T}}\, x_i(t) > 0, \qquad \text{for each} \quad i = 1,2,\ldots,n\,,$$

where $[0,T)$ is the maximal interval of existence of $x(t)$. In a like manner, (1.1.2) is said to <u>survive</u> if each solution $x(t)$ of (1.1.2) with $x(0) \in \mathrm{Int}\ (R_+^n)$ satisfies

$$(1.1.5)\qquad \underline{\lim_{t \to T}}\, x_i(t) > 0, \qquad \text{for each} \quad i = 1,2,\ldots,n\,,$$

where $[0, T)$ is as before.

Remark: An alternate, but related, definition of persistence is given in McGehee and Armstrong [17].

Our main purpose in this dissertation is to study the stability, persistence and the effect of evolution on predator-prey food chains with special emphasis on Lotka-Volterra food chains and food chains of length four.

§1.2 Mathematical Preliminaries

In this section we shall collect some results from ordinary differential equations and matrix theory which we shall have occasion to use in the following chapters. Definitions of the undefined terms and further details can be found in the references given.

(1) Dulac's Criterion: This criterion will be used in §4.6 to show the non-existence of a periodic orbit for Lotka-Volterra food chains of length two with a carrying capacity in the first species.

Statement of Criterion: Let

$$\left\{ \begin{array}{l} x_1' = f_1(x_1, x_2) \\ x_1' = f_2(x_1, x_2) \end{array} \right. \tag{1.2.1}$$

be a C^1 dynamic system and G a simply connected subregion of the domain of definition of system (1.2.1). Let $B(x_1, x_2)$ be a C^1 function defined in G such that the function

$$\frac{\partial}{\partial x_1}(B f_1) + \frac{\partial}{\partial x_2}(B f_2)$$

does not change sign. Then G contains no non-trivial periodic orbit of (1.2.1).

Reference: Andronov, Leontovich, Gordon and Maier [18], p. 205.

(2) Routh-Hurwicz Criterion: This criterion will be used in §3.2 and Chapter VI to obtain conditions for the asymptotic stability of the positive equilibrium.

Statement of Criterion: The table below lists necessary and sufficient conditions for every root of the real polynomial in the left column to have negative real part.

$\lambda^2 + a_1\lambda + a_2$	$a_1, a_2 > 0$
$\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3$	$a_1, a_3 > 0$ $a_1 a_2 > a_3$
$\lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + a_4$	$a_1, a_2, a_4 > 0$ $a_3(a_1 a_2 - a_3) > a_1^2 a_4$

Reference: Coppel [13], p. 158.

(3) Schwarz's Theorem: We shall use this theorem in §2.2 to study the asymptotic stability of the positive equilibrium of food chains whose variational matrix has a particular form.

Statement of Theorem: If a $n \times n$ matrix $A = [a_{ij}]$ can be transformed using a similarity transformation to the form

$$B = \begin{bmatrix} 0 & b_{12} & & & & & \\ -1 & \cdot & & & & & \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \\ & & & & & 0 & b_{n-1\,n} \\ & & & & & -1 & b_{n\,n} \end{bmatrix}$$

(so called Schwarz matrix), where the unspecified entries of B are all zero, then the number of eigenvalues of A which have positive real parts is equal to the number of positive members in the sequence

$$b_{n\,n};\ b_{n\,n}\,b_{n-1\,n},\ b_{n\,n}\,b_{n-1\,n}\,b_{n-2\,n-1},\ \ldots,\ \ldots,$$

$$\ldots,\ b_{n\,n}\,b_{n-1\,n}\ \cdots\ b_{23}\,b_{12}\ .$$

Remarks: (i) Transposing A along $\begin{bmatrix} & & \cdot \\ & \cdot & \\ \cdot & & \end{bmatrix}$, i.e., A becomes

$$\begin{bmatrix} a_{n\,n} & a_{n-1\,n} & \cdot & \cdot & \cdot & \cdot & a_{1\,n} \\ a_{n\,n-1} & \cdot & & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ a_{n\,1} & \cdot & & \cdot & \cdot & \cdot & a_{11} \end{bmatrix}$$

does not change its eigenvalues.

(ii) Eigenvalues of $-A$ are the negative of those of A.

(iii) For

$$T = (T_i; \alpha) = \begin{bmatrix} 1 & & & & & & \\ & \ddots & & & & & \\ & & 1 & & & & \\ & & & \frac{1}{\alpha} & & & \\ & & & & 1 & & \\ & & & & & \ddots & \\ & & & & & & 1 \end{bmatrix} \leftarrow i^{th}\ \text{row}$$

$$\uparrow$$

$$i^{th}\ \text{column}$$

$$TAT^{-1} = \begin{bmatrix} a_{11} & \cdots & \alpha a_{1i} & \cdots & a_{1n} \\ \vdots & & \vdots & & \vdots \\ \frac{1}{\alpha} a_{i1} & \cdots & a_{ii} & \cdots & \frac{1}{\alpha} a_{in} \\ \vdots & & \vdots & & \vdots \\ a_{n1} & \cdots & \alpha a_{ni} & \cdots & a_{nn} \end{bmatrix}$$

(iv) For

$$T = (T_{ij};\alpha) = \begin{bmatrix} 1 & & & & \\ & \ddots & & & \\ & & \alpha & & \\ & & & \ddots & \\ & & & & 1 \end{bmatrix} \leftarrow i^{th} \text{ row}$$

$$\uparrow$$

$$j^{th} \text{ column}$$

$$TAT^{-1} = \begin{bmatrix} a_{11} & \cdots & -\alpha a_{1i}+a_{1j} & \cdots & a_{1n} \\ \vdots & & \vdots & & \vdots \\ a_{i1}+\alpha a_{j1} & \cdots & -\alpha(a_{ii}+\alpha a_{ji})+(a_{ij}+\alpha a_{jj}) & \cdots & a_{in}+\alpha a_{jn} \\ \vdots & & \vdots & & \vdots \\ a_{n1} & & -\alpha a_{ni}+a_{nj} & \cdots & a_{nn} \end{bmatrix}$$

Reference: Schwarz [19] and Barnett and Storey [41], p. 52.

(4) Qualitative Stability Criterion: This criterion will be used in §2.2 and §3.2 to obtain necessary and sufficient conditions for the qualitative stability of the variational matrix.

Statement of Criterion: A $n \times n$ matrix $A = [a_{ij}]$ is qualitatively stable (i.e., matrices which are sign equivalent to A have all their eigenvalues with negative real parts) iff

(i) $a_{ii} \leq 0 \quad \forall_i \quad 1 \leq i \leq n$

and $\exists\, i$, such that $a_{ii} < 0$

(ii) $a_{ij}a_{ji} \leq 0 \quad \forall\ i \neq j$

(iii) $\forall\ i_1 \neq i_2 \neq i_3 \ldots \neq i_k \quad (k \geq 3)$

the product $a_{i_1 i_2}\, a_{i_2 i_3} \ldots a_{i_{k-1} i_k}\, a_{i_k i_1} = 0$

(iv) $\det A \neq 0$.

Reference: May [15], p. 71 and Quirk and Ruppert [20].

(5) Barbashin-Krasovskii's Theorem: We shall use this theorem in §4.6 to analyses the global stability of all the possible equilibra of Lotka-Volterra food chains of any length with a carrying capacity in the first species.

Statement of Theorem: Consider the vector differential equation

$$x' = F(x)$$

with $F : R^n \to R^n$ continuous and $F(0) = 0$. Let there exist an infinitely large positive definite function V such that the trajectory derivative V' of V satisfies

$$V' < 0 \qquad \text{outside } M$$

$$V' \leq 0 \qquad \text{on } M$$

where M $(\subset R^n)$ contains no entire trajectories except the equilibrium point $x = 0$. Then $x = 0$ is stable in the large.

Remark. This theorem can be trivially adapted to the case when the state space is not necessarily R^n.

Reference: Barbashin and Krasovskii [21] and Barbashin [22], p. 49.

§1.3 Outline of Thesis

In Chapter II, we discuss general food chains, in particular, we give some ecologically reasonable restrictions on the f_i's in (1.1.2) so that (1.1.2) can be used as an effective model for predator-prey food chains. Some general theorems on the stability and survivability of general food chains are also given. Chapter III is concerned with intermediate food chains. Boundedness of solution is proved in §3.1 whereas conditions for existence and stability of the equilibrium points of food chains of length four is stated in §3.2. In Chapter IV, we study the global stability of Lotka-Volterra food chains using a Liapunov function. We also illustrate the close relationship between stability and survivability in this particular case. Some easily obtained perturbation results are also given. Chapter V deals with the effect of selection on the equilibrium numbers of a food chain. Besides working out the details for food chains of length $n = 3, 4$, we also make some observations for food chains of an arbitrary length n. The three examples given in Chapter VI are used to illustrate the model possibilities in the controversal topic 'stability verses complexity'. Finally in Chapter VII, we make a brief summary of the results that we have obtained and discuss their significance.

CHAPTER II

GENERAL FOOD CHAINS

§2.1 Assumptions

Following Rescigno and Jones [1], we shall give a set of assumptions so that (1.1.2) can be used effectively to describe the dynamics of a 'straight' predator-prey food chain.

Verbally, the assumptions are:

(i) If predator and prey are both small in number, the prey will multiply (being unhindered by the small number of predators).

(ii) The prey cannot multiply over a certain population size (its carrying capacity), even in the absence of predators, due to limitation of its own food supply.

(iii) If the predator is too abundant, the prey cannot multiply.

(iv) Multiplication of the prey is slowed by an increase in the number of predators.

(v) For a constant predator/prey ratio, the multiplication of the prey (resp. the predator) is slowed (resp. accelerated) by an increase of the population size because the predator-prey encounters are more frequent.

(vi) If there are not enough prey, the predator cannot multiply.

(vii) Multiplication of the predator is slowed by an increase in its own numbers.

We now translate assumptions (i)-(vii) into mathematical restrictions on the f_i's in (1.1.2).

(1) Since we are only concerened with straight chains, i.e., x_2 preys on x_1, x_3 preys on x_2,..., and x_n preys on x_{n-1}, we have,

$$(2.1.1)\quad \begin{cases} f_1(x_1,x_2,\ldots,x_n) \equiv f_1(x_1,x_2) \\ f_2(x_1,x_2,\ldots,x_n) \equiv f_2(x_1,x_2,x_3) \\ f_3(x_1,x_2,\ldots,x_n) \equiv f_3(x_2,x_3,x_4) \\ \quad . \\ \quad . \\ \quad . \\ f_{n-1}(x_1,x_2,\ldots,x_n) \equiv f_{n-1}(x_{n-2},x_{n-1},x_n) \\ f_n(x_1,x_2,\ldots,x_n) \equiv f_n(x_{n-1},x_n) \end{cases}$$

(2) $\dfrac{\partial f_1}{\partial x_2} < 0, \quad \dfrac{\partial f_2}{\partial x_3} < 0, \quad \ldots, \quad \dfrac{\partial f_{n-1}}{\partial x_n} < 0$ (because of (iv)).

(3) $\left.\dfrac{\partial f_2}{\partial x_2}\right|_{x_3=0} < 0, \quad \left.\dfrac{\partial f_3}{\partial x_3}\right|_{x_4=0} < 0, \quad \ldots, \quad \left.\dfrac{\partial f_{n-1}}{\partial x_{n-1}}\right|_{x_n=0} < 0, \quad \dfrac{\partial f_n}{\partial x_n} < 0$

(because of (vii)).

Note that, for example, we require $\left.\dfrac{\partial f_2}{\partial x_2}\right|_{x_3=0} < 0$ instead of $\dfrac{\partial f_2}{\partial x_2} < 0$ because for $x_3 > 0$, increase in prey may satiate predators and thereby benefit the prey.

(4) $f_1(0,0) > 0$ (because of (i))

$\exists$ $A > 0$, such that $f_1(A,0) = 0$ (because of (ii)).

$\exists$ $B > 0$, such that $f_1(0,B) = 0$ (because of (iii)).

(5) $\exists$ $D > 0$, such that $f_n(D,0) = 0$ (because of (vi)).

(6) $\frac{\partial f_1}{\partial R_1} < 0$, $\frac{\partial f_2}{\partial R_2} < 0$, ..., $\frac{\partial f_{n-1}}{\partial R_{n-1}} < 0$, $\frac{\partial f_n}{\partial R_n} < 0$ where R_1 is the direction of the line $\frac{x_1}{x_2}$ = constant in the x_1-x_2 plane;

R_2 is the direction of the line $\frac{x_2}{x_3}$ = constant, x_1 = constant in the x_1-x_2-x_3 space;

.

.

.

R_{n-1} is the direction of the line $\frac{x_{n-1}}{x_n}$ = constant;

x_{n-2} = constant in the x_{n-2}-x_{n-1}-x_n space;

and R_n is the direction of the line $\frac{x_{n-1}}{x_n}$ = constant in the x_{n-1}-x_n plane

(because of (v)).

(7) $\exists\ S_1, S_2, \ldots, S_{n-2} > 0$ such that

$$(2.1.2) \qquad \begin{cases} f_2(S_1, 0, 0) = 0 \\ f_3(S_2, 0, 0) = 0 \\ \cdot \\ \cdot \\ \cdot \\ f_{n-1}(S_{n-2}, 0, 0) = 0 \end{cases}$$

(because of (vi)).

(8) $\exists$ strictly increasing functions

$$\begin{cases} k_3 : [S_1, \infty) \to R_+ \\ k_4 : [S_2, \infty) \to R_+ \\ \vdots \\ k_n : [S_{n-2}, \infty) \to R_+ \end{cases}$$

such that

$$\begin{cases} f_2(x_1, 0, k_3(x_1)) = 0 & \forall\ x_1 \geq S_1 \\ f_3(x_2, 0, k_4(x_2)) = 0 & \forall\ x_2 \geq S_2 \\ \vdots \\ f_{n-1}(x_{n-1}, 0, k_n(x_{n-2})) = 0 & \forall\ x_{n-2} \geq S_{n-2} \end{cases}$$

(because of (iii) and (vi)).

Remark: Although the assumptions given above are ecologically reasonable, they do not include all the food chain models studied in the literature; for example, the Lotka-Voterra food chain (see §4.1) is one important exception.

§2.2 A Stability Theorem

If assumption (1) of §2.1 holds, then (1.1.2) becomes

$$
(2.2.1)\qquad \begin{cases} x_1' = f_1(x_1,x_2) \\ x_2' = f_2(x_1,x_2,x_3) \\ x_3' = f_3(x_2,x_3,x_4) \\ \quad\vdots \\ x_{n-1}' = f_{n-1}(x_{n-2},x_{n-1},x_n) \\ x_n' = f_n(x_{n-1},x_n) \end{cases}
$$

Suppose (2.2.1) has a positive equilibrium x^*. Then the variational matrix M of (2.2.1) at x^* takes the form

$$
M = \begin{bmatrix} m_{11} & m_{12} & & & & & \\ m_{21} & m_{22} & m_{23} & & & & \\ & m_{32} & m_{33} & m_{34} & & & \\ & & & \ddots & & & \\ & & & & \ddots & & \\ & & & & & \ddots & \\ & & & & & m_{n-1\,n-2} \; m_{n-1\,n-1} & m_{n-1\,n} \\ & & & & & m_{n\,n-1} & m_{n\,n} \end{bmatrix}
$$

where all the unspecified entries of M are zero. Moreover, it is ecologically clear that we must have

$$m_{12}, m_{23}, \cdots, m_{n-1\,n} < 0$$

and

$$m_{21}, m_{32}, \cdots, m_{n\,n-1} > 0$$

The following theorem gives necessary and sufficient conditions for M to be qualitatively stable.

Theorem 2.2.1: M is qualitatively stable iff

$$m_{11}, m_{22}, \cdots, m_{n\,n} \leq 0$$

$$\exists\ i,\ 1 \leq i \leq n \quad \text{such that} \quad m_{ii} < 0$$

and

$$\det M \neq 0 .$$

Proof: It follows immediately from the qualitative stability criterion stated in §1.2 (4). □

Remark: Using induction (c.f., §5.3), one can show that for $m_{11}, m_{22}, \cdots, m_{nn} \leq 0$ then

(i) $$\det M \begin{cases} < 0 & \text{if } n \text{ is even} \\ \leq 0 & \text{if } n \text{ is odd} \end{cases}$$

and

(ii) if furthermore

$$m_{11} \text{ or } m_{33} \text{ or } \cdots \text{ or } m_{nn} < 0 ,$$

where n is odd, then $\det M < 0$.

Corollary 2.2.2: If $m_{11} < 0$ and $m_{22} = m_{33} = \ldots = m_{nn} = 0$ then M is qualitatively stable, and hence x* is asymptotically stable.

Proof: It will be proved in §5.3 that under the above assumptions

$$\det M \begin{cases} < 0 & \text{if } n \text{ is odd} \\ > 0 & \text{if } n \text{ is even} \end{cases}$$

The corollary then follows from the above theorem. □

Alternate Proof: We can transform -M into a Schwarz matrix as follows:

$$-M = \begin{bmatrix} -m_{11} & -m_{12} & & & & & & \\ -m_{21} & 0 & -m_{23} & & & & & \\ & -m_{32} & 0 & -m_{34} & & & & \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & & \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & & \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & -m_{n-1\,n-2} & 0 & -m_{n-1\,n} \\ & & & & & & -m_{n\,n-1} & 0 \end{bmatrix}$$

$$\xrightarrow{(T_2;m_{21})} \begin{bmatrix} -m_{11} & -m_{12}m_{21} & & & & & & \\ -1 & 0 & -\frac{m_{23}}{m_{21}} & & & & & \\ & -m_{21}m_{32} & 0 & -m_{34} & & & & \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & & \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & & \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & & \\ & & & & & & -m_{n-1\,n-2} & 0 & -m_{n-1\,n} \\ & & & & & & & -m_{n\,n-1} & 0 \end{bmatrix}$$

$$\xrightarrow{(T_3;m_{21}m_{32})}
\begin{bmatrix}
-m_{11} & -m_{12}m_{21} & & & & & & \\
-1 & 0 & -m_{23}m_{32} & & & & & \\
 & -1 & 0 & -\frac{m_{34}}{m_{21}m_{32}} & & & & \\
 & \cdot & \cdot & \cdot & \cdot\ \cdot\ \cdot & & & \\
 & \cdot & \cdot & \cdot & \cdot\ \cdot\ \cdot & & & \\
 & \cdot & \cdot & \cdot & \cdot\ \cdot\ \cdot & & & \\
 & & & & & -m_{n-1\ n-2} & 0 & -m_{n-1\ n} \\
 & & & & & & -m_{n\ n-1} & 0
\end{bmatrix}$$

$$\vdots\ \xrightarrow{\quad}
\begin{bmatrix}
-m_{11} & -m_{12}m_{21} & & & & & & \\
-1 & 0 & -m_{23}m_{32} & & & & & \\
 & -1 & 0 & -m_{34}m_{43} & & & & \\
 & \cdot & \cdot & \cdot & \cdot\ \cdot\ \cdot & & & \\
 & \cdot & \cdot & \cdot & \cdot\ \cdot\ \cdot & & & \\
 & \cdot & \cdot & \cdot & \cdot\ \cdot\ \cdot & & & \\
 & & & & & -1 & 0 & -m_{n-1\ n}\ m_{n\ n-1} \\
 & & & & & & -1 & 0
\end{bmatrix}$$

transpose along

$$\begin{bmatrix} & & & \\ & \ddots & & \\ & & & \end{bmatrix} \longrightarrow \begin{bmatrix} 0 & -m_{n-1\,n}\, m_{n\,n-1} & & & & \\ -1 & 0 & & & & \\ \cdot & \cdot & & \cdot\ \cdot\ \cdot & & \\ \cdot & \cdot & & \cdot\ \cdot\ \cdot & & \\ \cdot & \cdot & & \cdot\ \cdot\ \cdot & & \\ & & & & 0 & -m_{12}m_{21} \\ & & & & -1 & -m_{11} \end{bmatrix}$$

Since $-m_{11}$, $-m_{12}m_{21}$, $\cdots$, $-m_{n-1\,n}\, m_{n\,n-1} > 0$ therefore by Schwarz's theorem (§1.2 (3)), all eigenvalues of $-M$ have positive real parts and hence all eigenvalues of M have negative real parts. □

§2.3 General Theorems on Persistence and Survivability

Of the numerous ecosystem considerations, probably none affects ecosytem structure as drastically as the extinction of a biological species (e.g., Paine [23]). As demonstrated by public concern (Holden [24]) extinction of a biotic component of a food chain is topical as well as ecologically fundamental. It is the purpose of this section to state and prove some sufficiency theorems on persistence and survivability which are applicable to general food webs.

Definition: Let $w : R_+ \to R$ be continuous on R_+, C^1 on Int (R_+), and $w(0) = 0$. Suppose also that the interval of definition of every solution $y(t)$ of the differential equation

$$y' = w(y) \tag{2.3.1}$$

with $y(0) \in R_+$ can be extended to the whole semi axis $[0,\infty)$. Then

(i) (2.3.1) is said to be of <u>persistent type</u> if every solution $y(t)$ of (2.3.1) with $y(0) \in$ Int (R_+) satisfies

$$\lim_{t \to \infty} y(t) \quad 0 \ .$$

(ii) (2.3.1) is said to be of <u>extinction type</u> if every solution $y(t)$ of (2.3.1) with $y(0) \in$ Int (R_+) satisfies

$$\lim_{t \to \infty} y(t) = 0 \ .$$

Example: If $w(y) = ay$, then (2.3.1) is of persistence type whenever $a \geq 0$, and is of extinction type whenever $a < 0$.

Remark: (i) Since the initial value problem

$$y' = w(y) , \qquad y(0) \in R_+$$

has a unique solution, $\lim_{t \to \tau} y(t)$ always exists (may be $+\infty$).

(ii) There are, of course, functions w for which (2.3.1) is neither of persistent nor of extinction type.

Definition: Let $\rho : R_+^n \to R_+$ be continuous on R_+^n and C^1 on Int (R_+^n) and let $\rho'(x_1,\ldots,x_n) \equiv \sum_{i=1}^{n} \frac{\partial \rho}{\partial x_i} f_i(x_1,\ldots,x_n)$ be the trajectory derivative of ρ along (1.1.2). Then ρ is said to be a

(i) persistence function for (1.1.2) if

$$\rho(x_1,\ldots,x_n) \to 0 \qquad \text{whenever} \quad x_i \to 0$$

for some $i = 1,\ldots,n$; and, ρ' satisfies the inequality $\rho' \geq w(\rho)$ where w is of peristence type.

(ii) extinction function for (1.1.2) if

$$\rho(x_1,\ldots,x_n) \to 0 \qquad \text{only if} \quad x_i \to 0$$

for some $i = 1,\ldots,n$; and, ρ' satisfies the inequality $\rho' \leq w(\rho)$ where w is of extinction type.

(iii) survival function for (1.1.2) if

$$\rho(x_1^{(k)}, \ldots, x_n^{(k)}) \to 0 \qquad \text{as} \quad k \to \infty$$

whenever $x^{(k)} = (x_1^{(k)}, \ldots, x_n^{(k)}) \in R_+^n$ is a sequence with $x_i^{(k)} \to 0$ as $k \to \infty$ for some $i = 1,\ldots,n$; and, ρ' satisfies the inequality $\rho' \geq w(\rho)$ where w is of persistence type.

Theorem 2.3.1: (i) If there exists a persistence function for (1.1.2) then (1.1.2) is persistent.

(ii) If there exists an extinction function (1.1.2) then (1.1.2)

is non-persistent (i.e., (1.1.2) is not persistent).

(iii) If there exists a survival function for (1.1.2), then (1.1.2) survives.

Remark: Parts (i) and (ii) of the above theorem are due to Gard and Hallam [3].

Proof of Theorem: Since the proofs of all three parts (i), (ii) and (iii) are very similar, we shall only prove (iii).

Suppose (1.1.2) does not survive. Then there exists a solution $x(t)$ of (1.1.2) with $x(0) \in \text{Int}\,(R_+^n)$ such that

$$\exists\ i,\ 1 \le i \le n \quad \text{with} \quad \underline{\lim}_{t \to T^-} x_i(t) = 0$$

where $[0,T)$ is the maximal interval of definition of $x(t)$, i.e., there is a sequence $\{t_k\}$ with $t_k \to T$, such that

$$x_i(t_k) \to 0 \quad \text{as} \quad k \to \infty .$$

Since ρ is of persistent type, $\rho(x(t_k)) \to 0$ as $k \to \infty$. On the other hand, the differential inequality

$$\rho' \ge w(\rho)$$

implies $\rho(x(t)) \ge y(t)$ where $y(t)$ is the solution of the initial value problem

$$y' = w(y) , \quad y(0) = \rho(x(0))$$

This contradicts the fact that w is of persistent type. □

Remark: The merit of the above theorem is that it requires no prior information on the asymptotic behaviour of the solutions. However, as

in the case of Liapunov functions, it is in general not easy to construct a suitable persistent or survival function for (1.1.2).

CHAPTER III

INTERMEDIATE FOOD CHAINS

§3.1 Boundedness of Solutions

In this chapter, we shall discuss intermediate type food chain models studied by Freedman and Waltman [6] (see also Freedman [25]). They are of the form

$$(3.1.1)\quad \begin{cases} x_1' = x_1 g(x_1) - x_2 q_1(x_1) \\ x_2' = x_2(-d_2 + c_2 q_1(x_1)) - x_3 q_2(x_2) \\ \cdot \\ \cdot \\ \cdot \\ x_{n-1}' = x_{n-1}(-d_{n-1} + c_{n-1} q_{n-2}(x_{n-2})) - x_n q_{n-1}(x_{n-1}) \\ x_n' = x_n(-d_n + c_n q_{n-1}(x_{n-1})) \end{cases}$$

where (i) $g, q_1, \ldots, q_n : R_+ \to R$ are C^1

(ii) $g_{x_1}(x_1) \leq 0 \quad \forall\, x_1 \geq 0$

$g(0) = \alpha > 0$

(iii) $q_1(0) = \ldots = q_{n-1}(0) = 0$, and,

$$(3.1.2)\quad \begin{cases} q_{1\,x_1}(x_1) > 0 \quad \forall\, x_1 > 0 \\ \cdot \\ \cdot \\ \cdot \\ q_{n-1\,x_{n-1}}(x_{n-1}) > 0 \quad \forall\, x_{n-1} > 0 \end{cases}$$

(iv) $c_2, \ldots, c_n; d_2, \ldots, d_n > 0$

Note: $g_{x_1} = \frac{dg}{dx_1}$ and $q_i\, x_i = \frac{dq_i}{dx_i}$ $(i = 1,\ldots,n-1)$.

Here the d_i's $(i = 2,\ldots,n)$ is the death rate of the i^{th} species if left alone, g is the self-generating function for the primary producer x_1, p_i $(i = 1,\ldots,n-1)$ the predation function of the i^{th} species by the $(i+1)^{th}$ species and c_i $(i = 2,\ldots,n)$ is the efficency of predation.

It is clear that the two assumptions stated in §1.1 are satisfied, i.e., the initial value problem for (3.1.1) with initial condition $\epsilon\ R_+^n$ have a unique solution and that the hyperplanes H_i $(i = 1,\ldots,n)$ are invariant sets of (3.1.1). Moreover we have

Theorem 3.1.1: Under the assumption that

$$\exists\ K > 0 \quad \text{such that} \quad g(K) = 0$$

(i.e., there is a carrying capacity for x_1), every solution $x(t)$ of (3.1.1) with $x(0) \epsilon R_+^n$ is bounded. Consequently, $x(t)$ is defined on the whole semi-axis $[0,\infty)$.

Proof: Let $x(t)$ be a solution of (3.1.1) with $x(0) \epsilon R_+^n$. From the first equation of (3.1.1), we have

$$x_1' \leq x_1\, g(x_1) \quad .$$

Comparing this differential inequality with the scalar equation

$$x' = x\, g(x)$$

whose flow looks like

gives

$$(0 \leq)\ x_1(t) \leq \min\ (K,\ x_1(0)) \equiv \bar{x}_1 \ .$$

Define

$$A_{n-k+1} = \prod_{i=2}^{k} c_i \qquad (2 \leq k \leq n)$$

and

$$A_n = 1 \ .$$

Let

$$V = A_1x_1 + A_2x_2 + \ldots + A_nx_n \ .$$

Then

$$\begin{aligned} V' = A_1x_1' + A_2x_2' + \ldots + A_nx_n' &= [A_1x_1g(x_1) - A_1x_2q_1(x_1)] \\ &\quad + [A_2x_2(-d_2 + c_2q_1(x_1)) - A_2x_3q_2(x_2)] \\ &\quad + \ldots + A_nx_n(-d_n + c_nq_{n-1}(x_{n-1})) \\ &= -(d_2A_2x_2 + \ldots + d_nA_nx_n) + A_1x_1g(x_1) \\ &\leq -K(A_1x_1 + A_2x_2 + \ldots + A_nx_n) + A_1x_1g(x_1) + KA_1x_1 \end{aligned}$$

where

$$\begin{aligned} K &= \min\ (d_2, \ldots, d_n) \\ &\leq -KV + A_1\bar{x}_1g(\bar{x}_1) + KA_1\bar{x}_1 \ . \end{aligned}$$

Let

$$L = A_1\bar{x}_1g(\bar{x}_1) + KA_1\bar{x}_1 \ .$$

Then

$$[Ve^{Kt}]' = v'e^{Kt} + Kve^{Kt}$$

$$\leq L\, e^{Kt} \quad .$$

Integrating both sides gives

$$V(t)e^{Kt} - V(0) \leq L\, \frac{e^{Kt} - 1}{K}$$

$$\Longrightarrow V(t) \leq V(0) + \frac{L}{K} < \infty \quad .$$

Hence all the $x_1(t)$, $x_2(t)$, ..., $x_n(t)$, are bounded. □

Remark. This theorem was proved in Freedman and Waltman [6] for the case $n = 3$.

§3.2 Existence and Stability of Equilibria for n = 4

In this section we shall find conditions for the existence of equilibria of the intermediate food chain model (3.1.1) when n = 4 (which is the plant-herbivore-carnivore-secondary carnivore situation). Also, we shall discuss the asymptotic stability and the instability of these equilibria.

When n = 4, (3.1.1) becomes

$$(3.2.1)\quad \begin{cases} x_1' = x_1\, g(x_1) - x_2\, q_1(x_1) \\ x_2' = x_2\,(-d_2 + c_2\, q_1(x_1)) - x_3\, q_2(x_2) \\ x_3' = x_3\,(-d_3 + c_3\, q_2(x_2)) - x_4\, q_3(x_3) \\ x_4' = x_4\,(-d_4 + c_4\, q_3(x_3)) \quad . \end{cases}$$

Consider the system of equations

$$(3.2.2)\quad \begin{cases} x_1\, g(x_1) - x_2\, q_1(x_1) = 0 \\ x_2\,(-d_2 + c_2\, q_1(x_1)) - x_3\, q_2(x_2) = 0 \\ x_3\,(-d_3 + c_3\, q_2(x_2)) - x_4\, q_3(x_3) = 0 \\ x_4\,(-d_4 + c_4\, q_3(x_3)) = 0 \end{cases}$$

Since for $x_1, x_2, x_3, x_4 \geq 0$, $x_1 = 0 \Longrightarrow x_2 = 0 \Longrightarrow x_3 = 0 \Longrightarrow x_4 = 0$ in (3.2.2), therefore there are only five possible types of equilibrium points for (3.2.1), namely,

$$\begin{cases} E_0 = (0, 0, 0, 0) \\ E_1 = (\bar{x}_1, 0, 0, 0) \\ E_2 = (\tilde{x}_1, \tilde{x}_2, 0, 0) \\ E_3 = (\hat{x}_1, \hat{x}_2, \hat{x}_3, 0) \\ E_4 = (x_1^*, x_2^*, x_3^*, x_4^*) \end{cases}$$

where $\bar{x}_1, \tilde{x}_1, \tilde{x}_2, \hat{x}_1, \hat{x}_2, \hat{x}_3, x_1^*, x_2^*, x_3^*, x_4^*$ are all > 0.

The conditions for the existence and uniqueness of these equilibria are as follows:

(i) E_0 always exists and is unique.

(ii) E_1 exists iff $\exists\ K > 0$ such that $g(K) = 0$ and it is unique iff $g_{x_1}(K) < 0$. In that case, $\bar{x}_1 = K$.

(iii) E_2 exists iff $\frac{d_2}{c_2} \in \{q_1(x_1) : x_1 \geq 0\}$ and $\tilde{x}_1 < K$, if K exists, where $\tilde{x}_1 > 0$ is such that $q_1(\tilde{x}_1) = \frac{d_2}{c_2}$. Note that $\tilde{x}_2 = \frac{\tilde{x}_1\, g(\tilde{x}_1)}{q_1(\tilde{x}_1)}$ (> 0) and that E_2 is unique if it exists (since q_1 is strictly increasing).

(iv) E_3 exists if $\frac{d_3}{c_3} \in \{q_2(x_2) : x_2 \geq 0\}$

$$\hat{x}_2 \in \left\{ \frac{x_1\, g(x_1)}{q_1(x_1)} : x_1 > 0 \right\} \quad \text{and} \quad \tilde{x}_1 < \hat{x}_1$$

where $\hat{x}_2 > 0$ is such that $q_2(\hat{x}_2) = \frac{d_3}{c_3}$ and $\hat{x}_1 > 0$ is such that $\frac{\hat{x}_1\, g(\hat{x}_1)}{q_1(\hat{x}_1)} = \hat{x}_2$.

Note: $\hat{x}_3 = \dfrac{\hat{x}_2\,(-d_2 + c_2\, q_1(\hat{x}_1))}{q_2(x_2)}$ (> 0), the existence of $\tilde{x}_1$ is necessary for the existence of E_3 and if E_3 exists, then $\hat{x}_1 < K$ automatically (if K exists). Moreover, E_3 is unique iff the curves

$$y = \frac{x\, g(x)}{q_1(x)} \quad (x > 0) \quad \text{and} \quad y = \hat{x}_2$$

have only one intersection.

(v) E_4 exists iff

$$\frac{d_4}{c_4} \in \{q_3(x_3) : x_3 \geq 0\}$$

$$x_3^* \in \left\{ \frac{\dfrac{x_1\, g(x_1)}{q_1(x_1)}\,(-d_2 + c_2\, q_1(x_1))}{q_2\left(\dfrac{x_1\, g(x_1)}{p_1(x_1)}\right)} : x_1 \geq 0 \right\}$$

$x_1^* < K$ (if K exists) and $\hat{x}_2 < x_2^*$, where $x_3^* > 0$ is such that $q_3(x_3^*) = \dfrac{d_4}{c_4}$, $x_1^* > 0$ is such that

$$\frac{\dfrac{x_1^*\, g(x_1^*)}{q_1(x_1^*)}\,(-d_2 + c_2\, q_1(x_1^*))}{q_2\left(\dfrac{x_1^*\, g(x_1^*)}{q_1(x_1^*)}\right)} = x_3^*$$

and $x_2^* = \dfrac{x_1^*\, g(x_1^*)}{q_1(x_1^*)}$.

Note: $x_4^* = \dfrac{x_3^*\,(-d_3 + c_3\, q_2(x_2^*))}{q_3(x_3^*)}$ (> 0), the existence of $\hat{x}_2$ is necessary for the existence of E_4 and if E_4 exists then $\tilde{x}_1$ exists

automatically and we have $\tilde{x}_1 < x_1^*$. Moreover, E_4 is unique iff the curves

$$y = \frac{\frac{x\, g(x)}{q_1(x)}\,(-d_2^* + c_2\, q_1(x))}{q_2\left(\frac{x\, g(x)}{q_1(x)}\right)} \qquad (x > \tilde{x}_1)$$

and $y = x_3^*$ have only one intersection.

To study the stability of these equilibria, we consider the variational matrix of (3.2.1) given by:

$$M = \begin{bmatrix} x_1 g_{x_1}(x_1) + g(x_1) - x_2 q_{1\,x_1}(x_1) & -q_1(x_1) & 0 & 0 \\ c_2 x_2 q_{1\,x_1}(x_1) & -d_2 + c_2 q_1(x_1) - x_3 q_{2\,x_2}(x_2) & -q_2(x_2) & 0 \\ 0 & c_3 x_3 q_{2\,x_2}(x_2) & -d_3 + c_3 q_2(x_2) x_4 q_{3\,x_3}(x_3) & -q_3(x_3) \\ 0 & 0 & c_4 x_4 q_{3\,x_3}(x_3) & -d_4 + c_4 q_3(x_3) \end{bmatrix}$$

At E_0,

$$M = \begin{bmatrix} \alpha & 0 & 0 & 0 \\ 0 & -d_2 & 0 & 0 \\ 0 & 0 & -d_3 & 0 \\ 0 & 0 & 0 & -d_4 \end{bmatrix}$$

therefore E_0 is unstable.

At E_1,

$$M = \begin{bmatrix} K\, g_{x_1}(K) & -q_1(K) & 0 & 0 \\ 0 & -d_2+c_2q_1(K) & 0 & 0 \\ 0 & 0 & -d_3 & 0 \\ 0 & 0 & 0 & -d_4 \end{bmatrix}$$

therefore E_1 is unstable if $-d_2+c_2q_1(K) > 0$ (i.e., E_2 or E_4 exist) and is asymptotically stable if $-d_2+c_2q_1(K) < 0$ and $g_{x_1}(K) < 0$, (i.e., E_1 unique).

At E_2,

$$M = \begin{bmatrix} \tilde{x}_1 g_{x_1}(\tilde{x}_1)+g(\tilde{x}_1)-\tilde{x}_2 q_{1\,x_1}(\tilde{x}_1) & -q_1(\tilde{x}_1) & 0 & 0 \\ c_2\tilde{x}_2 q_{1\,x_1}(\tilde{x}_1) & 0 & -q_2(\tilde{x}_2) & 0 \\ 0 & 0 & -d_3+c_3q_2(\tilde{x}_2) & 0 \\ 0 & 0 & 0 & -d_4 \end{bmatrix}$$

$$= \begin{bmatrix} \tilde{m}_{11} & \tilde{m}_{12} & 0 & 0 \\ \tilde{m}_{21} & 0 & \tilde{m}_{23} & 0 \\ 0 & 0 & \tilde{m}_{33} & 0 \\ 0 & 0 & 0 & \tilde{m}_{44} \end{bmatrix}$$

where $\tilde{m}_{11} = \tilde{x}_1 \, g_{x_1}(\tilde{x}_1) + g(\tilde{x}_1) - \tilde{x}_2 \, q_{1\,x_1}(\tilde{x}_1)$

$\tilde{m}_{12} < 0$, $\tilde{m}_{21} > 0$, $\tilde{m}_{23} < 0$

$\tilde{m}_{33} = -d_3 + c_3 \, q_2(\tilde{x}_2)$ $(= 0$ iff $\tilde{x}_2 = \hat{x}_2$; < 0 iff $\hat{x}_2$ does not exist or $\tilde{x}_2 < \hat{x}_2$; > 0 iff $\tilde{x}_2 > \hat{x}_2)$

$\tilde{m}_{44} < 0$.

Now

$$\det \begin{bmatrix} \tilde{m}_{11}-\lambda & \tilde{m}_{12} & 0 & 0 \\ \tilde{m}_{21} & -\lambda & \tilde{m}_{23} & 0 \\ 0 & 0 & \tilde{m}_{33}-\lambda & 0 \\ 0 & 0 & 0 & \tilde{m}_{44}-\lambda \end{bmatrix}$$

$$= (\tilde{m}_{11}-\lambda) \det \begin{bmatrix} -\lambda & \tilde{m}_{23} & 0 \\ 0 & \tilde{m}_{33}-\lambda & 0 \\ 0 & 0 & \tilde{m}_{44}-\lambda \end{bmatrix} - \tilde{m}_{12} \det \begin{bmatrix} \tilde{m}_{21} & \tilde{m}_{23} & 0 \\ 0 & \tilde{m}_{33}-\lambda & 0 \\ 0 & 0 & \tilde{m}_{44}-\lambda \end{bmatrix}$$

$$= (\tilde{m}_{11}-\lambda)(-\lambda)(\tilde{m}_{33}-\lambda)(\tilde{m}_{44}-\lambda) - \tilde{m}_{12} \, \tilde{m}_{21} \, (\tilde{m}_{33}-\lambda)(\tilde{m}_{44}-\lambda) \, .$$

Therefore the eigenvalues of M are $\lambda = \tilde{m}_{33}, \tilde{m}_{44}$ and the roots of

$$\lambda^2 - \tilde{m}_{11}\lambda - \tilde{m}_{12}\,\tilde{m}_{21} = 0$$

$$\text{i.e.,} \quad \lambda = \frac{\tilde{m}_{11} \pm \sqrt{\tilde{m}_{11}^2 + 4\tilde{m}_{12}\,\tilde{m}_{21}}}{2} \quad .$$

Since $\tilde{m}_{12}\,\tilde{m}_{21} < 0$,

$\tilde{m}_{11} = 0 \Longrightarrow$ 2 imaginary roots

$\tilde{m}_{11} < 0 \Longrightarrow$ both roots have negative real parts

$\tilde{m}_{11} > 0 \Longrightarrow$ both roots have positive real parts

hence,

(i) if $\tilde{m}_{11}$ or $\tilde{m}_{33} > 0$, then E_2 is unstable

(ii) if $\tilde{m}_{11}$ and $\tilde{m}_{33} < 0$, then E_2 is asymptotically stable.

At E_3,

$$M = \begin{bmatrix} \hat{x}_1 g_{x_1}(\hat{x}_1) + g(\hat{x}_1) - \hat{x}_2 q_{1\,x_1}(\hat{x}_1) & -q_1(\hat{x}_1) & 0 & 0 \\ c_2 \hat{x}_2 q_{1\,x_1}(\hat{x}_1) & -d_2 + c_2 q_1(\hat{x}_1) - \hat{x}_3 q_{2\,x_2}(\hat{x}_2) & -q_2(\hat{x}_2) & 0 \\ 0 & c_3 \hat{x}_3 q_{2\,x_2}(\hat{x}_2) & 0 & -q_3(\hat{x}_3) \\ 0 & 0 & 0 & -d_4 + c_4 q_3(\hat{x}_3) \end{bmatrix}$$

$$= \begin{bmatrix} \hat{m}_{11} & \hat{m}_{12} & 0 & 0 \\ \hat{m}_{21} & \hat{m}_{22} & \hat{m}_{23} & 0 \\ 0 & \hat{m}_{32} & 0 & \hat{m}_{34} \\ 0 & 0 & 0 & \hat{m}_{44} \end{bmatrix}$$

where $\hat{m}_{11} = \hat{x}_1 \, g_{x_1}(\hat{x}_1) + g(\hat{x}_1) - \hat{x}_2 \, q_{1\,x_1}(\hat{x}_1)$

$\hat{m}_{12} < 0, \quad \hat{m}_{21} > 0$

$\hat{m}_{22} = -d_2 + c_2 \, q_1(\hat{x}_1) - \hat{x}_3 \, q_{2\,x_2}(\hat{x}_2)$

$\hat{m}_{23} < 0, \quad \hat{m}_{32} > 0, \quad \hat{m}_{34} < 0$

$\hat{m}_{44} = -d_4 + c_4 \, q_3(\hat{x}_3)$

$(= 0$ iff $\hat{x}_3 = x_3^*$; < 0 iff x_3^* does not exist or

$\hat{x}_3 < x_3^*$; > 0 iff $x_3 > x_3^*)$.

Clearly the eigenvalues of M are $\lambda = \hat{m}_{44}$ and the roots of

$$\det \begin{bmatrix} \hat{m}_{11}-\lambda & \hat{m}_{12} & 0 \\ \hat{m}_{21} & \hat{m}_{22}-\lambda & \hat{m}_{23} \\ 0 & \hat{m}_{32} & -\lambda \end{bmatrix} = 0$$

i.e., $f(\lambda) \equiv \lambda^3 - (\hat{m}_{11}+\hat{m}_{22})\lambda^2 + (\hat{m}_{11}\hat{m}_{22}-\hat{m}_{23}\hat{m}_{32}-\hat{m}_{12}\hat{m}_{21})\lambda + \hat{m}_{11}\hat{m}_{23}\hat{m}_{32} = 0.$

Note: $f(0) = \hat{m}_{11}\hat{m}_{23}\hat{m}_{32}$.

Case 1: $\hat{m}_{11} > 0$. Then $f(0) < 0$, so that $f(\lambda) = 0$ has a positive root.

Case 2: $\hat{m}_{11} = 0$. Then $f(0) = 0$, so that $\lambda = 0$ is a root of $f(\lambda) = 0$. Factoring out λ from $f(\lambda) = 0$, we have

$$\lambda^2 - (\hat{m}_{11}+\hat{m}_{22})\lambda + (\hat{m}_{11}\hat{m}_{22} - \hat{m}_{23}\hat{m}_{32} - \hat{m}_{12}\hat{m}_{21}) = 0$$

or

$$\lambda^2 - \hat{m}_{22}\lambda - (\hat{m}_{23}\hat{m}_{32} + \hat{m}_{12}\hat{m}_{21}) = 0$$

whose roots are

$$\lambda = \frac{\hat{m}_{22} \pm \sqrt{\hat{m}_{22}^2 + 4(\hat{m}_{23}\hat{m}_{32} + \hat{m}_{12}\hat{m}_{21})}}{2} .$$

Since $\hat{m}_{23}\hat{m}_{32} + \hat{m}_{12}\hat{m}_{21} < 0$,

$\hat{m}_{22} = 0$ ⟹ 2 imaginary roots

$\hat{m}_{22} < 0$ ⟹ both roots have negative real parts

$\hat{m}_{22} > 0$ ⟹ both roots have positive real parts.

Case 3: $\hat{m}_{11} < 0$. Then $f(0) > 0$, so that $f(\lambda) = 0$ has a negative root. We can transform

$$\begin{bmatrix} \hat{m}_{11} & \hat{m}_{12} & 0 \\ \hat{m}_{21} & \hat{m}_{22} & \hat{m}_{23} \\ 0 & \hat{m}_{32} & 0 \end{bmatrix}$$

into the Schwarz form as follows:

$$\begin{bmatrix} \hat{m}_{11} & \hat{m}_{12} & 0 \\ \hat{m}_{21} & \hat{m}_{22} & \hat{m}_{23} \\ 0 & \hat{m}_{32} & 0 \end{bmatrix} \xrightarrow{\text{transpose along } \begin{bmatrix} & & \\ & \ddots & \\ & & \end{bmatrix}} \begin{bmatrix} 0 & \hat{m}_{23} & 0 \\ \hat{m}_{32} & \hat{m}_{22} & \hat{m}_{12} \\ 0 & \hat{m}_{21} & \hat{m}_{11} \end{bmatrix}$$

$$\xrightarrow{(T_{21};-\hat{m}_{32})}\begin{bmatrix} 0 & -\hat{m}_{23}\hat{m}_{32} & 0 \\ -1 & \hat{m}_{22} & -\dfrac{\hat{m}_{12}}{\hat{m}_{32}} \\ 0 & -\hat{m}_{21}\hat{m}_{23} & \hat{m}_{11} \end{bmatrix} \xrightarrow{(T_3;\hat{m}_{21}\hat{m}_{32})} \begin{bmatrix} 0 & -\hat{m}_{23}\hat{m}_{32} & 0 \\ -1 & \hat{m}_{22} & -\hat{m}_{12}\hat{m}_{21} \\ 0 & -1 & \hat{m}_{11} \end{bmatrix}$$

$$\xrightarrow{(T_{23};m_{22})}\begin{bmatrix} 0 & -\hat{m}_{23}\hat{m}_{32} & 0 \\ -1 & 0 & \hat{m}_{11}\hat{m}_{22} - \hat{m}_{12}\hat{m}_{21} \\ 0 & -1 & \hat{m}_{11} \end{bmatrix} - - > \begin{bmatrix} 0 & -\hat{m}_{23}\hat{m}_{32} & \hat{m}_{22}\hat{m}_{23}\hat{m}_{32} \\ -1 & 0 & \hat{m}_{11}\hat{m}_{22} - \hat{m}_{12}\hat{m}_{21} \\ 0 & -1 & \hat{m}_{11} + \hat{m}_{22} \end{bmatrix}$$

$$\xrightarrow[\text{(supposing } \hat{m}_{11}+\hat{m}_{22} \neq 0)]{\left(T_{13};\ \frac{\hat{m}_{22}\hat{m}_{23}\hat{m}_{32}}{\hat{m}_{11}+\hat{m}_{22}}\right)} \begin{bmatrix} 0 & -\hat{m}_{23}\hat{m}_{32} + \dfrac{\hat{m}_{22}\hat{m}_{23}\hat{m}_{32}}{\hat{m}_{11}+\hat{m}_{22}} & 0 \\ -1 & 0 & \hat{m}_{11}\hat{m}_{22} - \hat{m}_{12}\hat{m}_{21} \\ 0 & -1 & \hat{m}_{11} + \hat{m}_{22} \end{bmatrix}$$

$$\cdot \quad \begin{bmatrix} 0 & -\hat{m}_{23}\hat{m}_{32} + \dfrac{\hat{m}_{22}\hat{m}_{23}\hat{m}_{32}}{\hat{m}_{11}+\hat{m}_{22}} & 0 \\ -1 & 0 & \hat{m}_{11}\hat{m}_{22} - \hat{m}_{12}\hat{m}_{21} - \dfrac{\hat{m}_{22}\hat{m}_{23}\hat{m}_{32}}{\hat{m}_{11}+\hat{m}_{22}} \\ 0 & -1 & \hat{m}_{11}+\hat{m}_{22} \end{bmatrix}$$

Subcase 3.1: $\hat{m}_{11} + \hat{m}_{22} > 0$. By Schwarz's theorem (§1.2 (3)), $f(\lambda) = 0$ has at least one root which has positive real part.

Subcase 3.2: $\hat{m}_{11} + \hat{m}_{22} = 0$. Then

$$f(\lambda) = \lambda^3 + (\hat{m}_{11}\hat{m}_{22} - \hat{m}_{23}\hat{m}_{32} - \hat{m}_{12}\hat{m}_{21})\lambda + \hat{m}_{11}\hat{m}_{23}\hat{m}_{32} \quad .$$

Let $a < 0$ be a negative root of $f(\lambda) = 0$. We can factorise $f(\lambda) = 0$ into

$$(\lambda - a)(\lambda^2 + b\lambda + c) = 0$$

or

$$\lambda^3 + (b-a)\lambda^2 + (c-ab)\lambda - ac = 0 \quad .$$

Comparing coefficients we have,

$$b - a = 0$$

$$c - ab = \hat{m}_{11}\hat{m}_{22} - \hat{m}_{23}\hat{m}_{32} - \hat{m}_{12}\hat{m}_{21}$$

and

$$-ac = \hat{m}_{11}\hat{m}_{23}\hat{m}_{32}$$

so that

$$b = a < 0 \qquad \text{and} \qquad c = \frac{\hat{m}_{11}\hat{m}_{23}\hat{m}_{32}}{-a} > 0 \quad .$$

Hence both roots of

$$\lambda^2 + b\lambda + c = 0$$

have positive real parts.

Subcase 3.3: $\hat{m}_{11} + \hat{m}_{22} < 0$. Note that

$$-\hat{m}_{23}\hat{m}_{32} + \frac{\hat{m}_{22}\hat{m}_{23}\hat{m}_{32}}{\hat{m}_{11} + \hat{m}_{22}} = -\frac{\hat{m}_{11}\hat{m}_{23}\hat{m}_{32}}{\hat{m}_{11} + \hat{m}_{22}} > 0 \quad .$$

Again by the Schwarz's theorem,

$$\hat{m}_{11}\hat{m}_{22} - \hat{m}_{12}\hat{m}_{21} - \frac{\hat{m}_{22}\hat{m}_{23}\hat{m}_{32}}{\hat{m}_{11} + \hat{m}_{22}} \begin{cases} > 0 \Longrightarrow \text{all three roots have negative real parts} \\ = 0 \Longrightarrow \text{one negative root, the other two have zero real parts} \\ < 0 \Longrightarrow \text{one negative root, the other two have positive real parts.} \end{cases}$$

Hence,

(i) if $\hat{m}_{44}$ or $\hat{m}_{11}$ or $\hat{m}_{11}+\hat{m}_{22} > 0$, then E_3 is unstable,

(ii) if $\hat{m}_{11} < 0$ and $\hat{m}_{11}+\hat{m}_{22} = 0$ or $\hat{m}_{11} < 0$, $\hat{m}_{11}+\hat{m}_{22} < 0$ and

$$\hat{m}_{11}\hat{m}_{22} - \hat{m}_{12}\hat{m}_{21} - \frac{\hat{m}_{22}\hat{m}_{23}\hat{m}_{32}}{\hat{m}_{11} + \hat{m}_{22}} < 0 \quad \text{then } E_3 \text{ is unstable.}$$

(iii) if $\hat{m}_{44} < 0$, $\hat{m}_{11}+\hat{m}_{44} < 0$ and $\hat{m}_{11}\hat{m}_{22} - \hat{m}_{12}\hat{m}_{21} - \frac{\hat{m}_{22}\hat{m}_{23}\hat{m}_{32}}{\hat{m}_{11} + \hat{m}_{22}} > 0$

then E_3 is asymptotically stable.

At E_4,

$$M = \begin{bmatrix} x_1^* g_{x_1}(x_1^*) + g(x_1^*) - x_2^* q_1 \, x_1(x_1^*) & -q_1(x_1^*) & 0 & 0 \\ c_2 x_2^* q_1 \, x_1(x_1^*) & -d_2 + c_2 q_1(x_1^*) - x_3^* q_2 \, x_2(x_2^*) & -q_2(x_2^*) & 0 \\ 0 & c_3 x_3^* q_2 \, x_2(x_2^*) & -d_3 + c_3 q_2(x_2^*) - x_4^* q_3 \, x_3(x_3^*) & -q_3(x_3^*) \\ 0 & 0 & 0 & -d_4 + c_4 q_3(x_3^*) \end{bmatrix}$$

$$= \begin{bmatrix} m_{11} & m_{12} & 0 & 0 \\ m_{21} & m_{22} & m_{23} & 0 \\ 0 & m_{32} & m_{33} & m_{34} \\ 0 & 0 & m_{43} & 0 \end{bmatrix}$$

where $m_{11} = x_1^* g_{x_1}(x_1^*) + g(x_1^*) - x_2^* q_1 \, x_1^{(x_1^*)}$

$m_{12} < 0, \quad m_{21} > 0$

$m_{22} = -d_2 + c_2 q_1(x_1^*) - x_3^* q_2 \, x_2^{(x_2^*)}$

$m_{23} < 0, \quad m_{32} > 0$

$m_{33} = -d_3 + c_3 q_2(x_2^*) - x_4^* q_3 \, x_3^{(x_3^*)}$

$m_{34} < 0, \quad m_{43} > 0$.

The characteristic equation of M is

$$\det \begin{bmatrix} m_{11}-\lambda & m_{12} & 0 & 0 \\ m_{21} & m_{22}-\lambda & m_{23} & 0 \\ 0 & m_{32} & m_{33}-\lambda & m_{43} \\ 0 & 0 & m_{43} & -\lambda \end{bmatrix} = 0$$

or

$$(m_{11}-\lambda) \det \begin{bmatrix} m_{22}-\lambda & m_{23} & 0 \\ m_{32} & m_{33}-\lambda & m_{34} \\ 0 & m_{43} & -\lambda \end{bmatrix}$$

$$-m_{12} \det \begin{bmatrix} m_{21} & m_{23} & 0 \\ 0 & m_{33}-\lambda & m_{34} \\ 0 & m_{43} & -\lambda \end{bmatrix} = 0$$

or

$$(m_{11}-\lambda)[(m_{22}-\lambda)(m_{33}-\lambda)(-\lambda) - m_{34}m_{43}(m_{22}-\lambda) + m_{23}m_{32}\lambda]$$
$$- m_{12}[m_{21}(m_{33}-\lambda)(-\lambda) - m_{21}m_{34}m_{43}] = 0$$

or

$$(m_{11}-\lambda)[-\lambda^3 + (m_{22}+m_{33})\lambda^2 + (-m_{22}m_{33} + m_{23}m_{32} + m_{43}m_{43})\lambda - m_{22}m_{34}m_{43}]$$
$$-m_{12}[-m_{21}m_{33}\lambda + m_{21}\lambda^2 - m_{21}m_{34}m_{43}] = 0$$

or

$$\lambda^4 - (m_{11}+m_{22}+m_{33})\lambda^3 + (m_{11}m_{22}+m_{11}m_{33}+m_{22}m_{33}-m_{23}m_{32}-m_{34}m_{43}-m_{12}m_{21})\lambda^2$$
$$+ (m_{22}m_{34}m_{43} - m_{11}m_{22}m_{33} + m_{11}m_{23}m_{32} + m_{11}m_{34}m_{43} + m_{12}m_{21}m_{33})\lambda$$
$$+ (-m_{11}m_{22}m_{34}m_{43} + m_{12}m_{21}m_{34}m_{43}) = 0$$

or

$$\lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + a_4 = 0$$

where

$$a_1 = -(m_{11}+m_{22}+m_{33})$$

$$a_2 = m_{11}m_{22} + m_{11}m_{33} + m_{22}m_{33} - m_{23}m_{32} - m_{34}m_{43} - m_{12}m_{21}$$

$$a_3 = m_{22}m_{34}m_{43} - m_{11}m_{22}m_{33} + m_{11}m_{23}m_{32} + m_{11}m_{34}m_{43} + m_{12}m_{21}m_{33}$$

$$a_4 = -m_{11}m_{22}m_{34}m_{43} + m_{12}m_{21}m_{34}m_{43}$$

By the Routh-Hurwicz criterion, (§1.2 (2)), all roots of

$$\lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + a_4 = 0$$

will have negative real parts iff

$$a_1, a_2, a_4 > 0 \quad \text{and} \quad a_3(a_1a_2 - a_3) > a_1^2 a_4 .$$

Now, $a_1 > 0$ gives

(3.2.3) $$m_{11}+m_{22}+m_{33} < 0$$

$a_2 > 0$ gives

(3.2.4) $$m_{11}m_{22}+m_{11}m_{33}+m_{22}m_{33} > m_{23}m_{32}+m_{34}m_{43}+m_{12}m_{21}$$

$a_4 > 0$ gives

$$m_{12}m_{21}m_{34}m_{43} > m_{11}m_{22}m_{34}m_{43} \quad \text{or}$$

(3.2.5) $$m_{12}m_{21} < m_{11}m_{22}$$

and $a_3(a_1a_2 - a_3) > a_1^2 a_4$ gives

$$\begin{aligned}
&m_{22}^2m_{23}m_{32}m_{34}m_{43} + m_{22}m_{23}m_{32}m_{33}m_{34}m_{43} + m_{22}m_{33}m_{34}^2m_{43}^2 \\
&+ m_{11}^3m_{22}^2m_{33} + m_{11}^3m_{22}m_{33}^2 + m_{11}^2m_{22}^3m_{33} + m_{11}m_{22}^3m_{33}^2 \\
&+ 2m_{11}^2m_{22}^2m_{33}^2 + m_{11}^2m_{22}m_{33}^2 + m_{11}m_{22}^2m_{33}^2 + m_{11}^2m_{12}m_{21}m_{23}m_{32} \\
&+ m_{11}m_{22}m_{23}^2m_{32}^2 + m_{11}m_{12}m_{21}m_{22}m_{23}m_{32} + m_{11}m_{23}^2m_{32}^2m_{33} \\
&+ 2m_{11}m_{23}m_{32}m_{33}m_{34}m_{43} + m_{11}m_{22}m_{23}m_{32}m_{34}m_{43} + m_{11}m_{33}m_{34}^2m_{34}^2 \\
&+ m_{11}^2m_{12}^2m_{21}m_{33} + m_{12}m_{21}m_{22}m_{23}m_{32}m_{33} + m_{12}^2m_{21}^2m_{22}m_{33} \\
&+ m_{12}m_{21}m_{23}m_{32}m_{33}^2 \\
&>
\end{aligned}$$

$$m_{22}^3 m_{33} m_{34} m_{43} + m_{22}^2 m_{33}^2 m_{34} m_{43} + 2m_{11}^2 m_{12} m_{21} m_{22} m_{33}$$

$$+ 2m_{11} m_{22}^2 m_{23} m_{32} m_{33} + 2m_{11} m_{12} m_{21} m_{22} m_{33}^2 + 2m_{11} m_{22} m_{23} m_{32} m_{33}^2$$

$$+ 2m_{11} m_{22} m_{33}^2 m_{34} m_{43} + m_{11}^3 m_{22} m_{23} m_{32} + m_{11}^3 m_{23} m_{32} m_{33} + m_{11}^2 m_{22}^2 m_{23} m_{32}$$

$$+ m_{11}^2 m_{22} m_{23} m_{32} m_{33} + m_{11}^2 m_{22} m_{23} m_{32} m_{33} + m_{11}^2 m_{23} m_{32} m_{33}^2$$

$$+ m_{11}^3 m_{33} m_{34} m_{43} + m_{11} m_{22}^2 m_{33} m_{34} m_{43} + m_{11}^2 m_{22} m_{33} m_{34} m_{43}$$

$$+ m_{11}^2 m_{33}^2 m_{34} m_{43} + m_{11}^2 m_{12} m_{21} m_{33}^2 + m_{11} m_{12} m_{21} m_{22}^2 m_{33}$$

$$+ m_{12} m_{21} m_{22}^2 m_{33}^2 + m_{11} m_{12} m_{21} m_{22} m_{33}^2 + m_{11} m_{12} m_{21} m_{33}^3 + m_{12} m_{21} m_{22} m_{33}^3$$

$$+ 2m_{12} m_{21} m_{22} m_{33} m_{34} m_{43} + 2m_{11} m_{12} m_{21} m_{33} m_{34} m_{43}$$

(3.2.6)

Hence, E_4 will be asymptotically stable if (3.2.3), (3.2.4), (3.2.5) and (3.2.6) hold. We also have the sharper result

Theorem 3.2.1: M is qualitatively stable iff

$$m_{11},\ m_{22},\ \text{and}\ m_{33} \leq 0$$

and

$$\text{at least one } m_{ii} \quad (i = 1,2,3) < 0 .$$

Proof: Note that $m_{11} m_{22} \neq m_{12} m_{21}$ is equivalent to the condition that 0 not be a characteristic root of M (i.e., det $M \neq 0$), which is guaranteed by the above conditions (since, in that case $m_{11} m_{22} \geq 0$). The remainder of the proof follows from Theorem 2.2.1. □

CHAPTER IV

LOTKA-VOLTERRA FOOD CHAINS WITH OR WITHOUT CARRYING CAPACITY

§4.1 Introduction

Lotka-Volterra dynamics has been extensively studied by many authors. Besides the classic works of Volterra [26] and Lotka [27], one may also refer to D'Ancona [28], Kerner [29], Goel, Maitra and Montroll [30], Rescigno and Richardson [31], and Goh [32]. In this chapter, we shall consider Lotka-Volterra food chains of the form

$$
(4.1.1)\quad \begin{cases}
x_1' = x_1(a_{10} - a_{11}x_1 - a_{12}x_2) \\
x_2' = x_2(-a_{20} + a_{21}x_1 - a_{22}x_2 - a_{23}x_3) \\
x_3' = x_3(-a_{30} + a_{32}x_2 - a_{33}x_3 - a_{34}x_4) \\
\cdot \\
\cdot \\
\cdot \\
x_{n-1}' = x_{n-1}(-a_{n-1\,0} + a_{n-1\,n-2}x_{n-2} - a_{n-1\,n-1}x_{n-1} - a_{n-1\,n}x_n) \\
x_n' = x_n(-a_{n0} + a_{n\,n-1}x_{n-1} - a_{n\,n}x_n)
\end{cases}
$$

where all the specified a_{ij} are > 0, except $a_{11}, a_{22}, \cdots, a_{nn}$ which are ≥ 0.

Our purpose is to study the stability of the equilibria of (4.1.1) and to improve some of the persistence results given in Gard and Hallam [3] to survivability.

It is clear that the two assumptions given in §1.1 hold

for (4.1.1), i.e.,

$\forall\, x_0 \in R_+^n$, there exists a unique solution $x(t)$ of (4.1.1) such that $x(0) = x_0$

and that H_i $(i = 1,\ldots,n)$ are invariant sets of (4.1.1).

Moreover, we have

Theorem 4.1.1: If $a_{11} > 0$, then every solution of (4.1.1) with initial condition $\in R_+^n$ is bounded.

Proof: (Similar to Theorem 3.1.1). □

§4.2 A Liapunov Function

Lemma 4.2.1: System (4.1.1) can be rewritten as

$$(4.2.1) \qquad x_i' = x_i(\epsilon_i - \lambda_i x_i + \frac{1}{\beta_i}\sum_{j=1}^{n} \alpha_{ij} x_j) \qquad (i = 1,\ldots,n)$$

where $\epsilon_1 = a_{10}$, $\epsilon_2 = -a_{20},\ldots,\epsilon_n = -a_{n0}$

$$\lambda_i = a_{ii} \quad (i = 1,\ldots,n), \qquad \beta_i > 0 \quad (i = 1,\ldots,n)$$

and $[\alpha_{ij}]$ is anti-symmetric.

Proof: From the first equation of (4.1.1), choose

$$\frac{1}{\beta_1} = 1 \qquad \text{and} \qquad \alpha_{12} = -a_{12}$$

From the second equation of (4.1.1), choose

$$\frac{1}{\beta_2} = \frac{a_{21}}{a_{12}} \qquad \text{and} \qquad \alpha_{23} = -a_{12}\frac{a_{23}}{a_{21}}$$

etc.

In general, choose

$$\beta_i = 1\,\frac{a_{12}}{a_{21}} \cdots \frac{a_{i-1\,i}}{a_{i\,i-1}} \qquad (i = 1,2,\ldots,n)$$

$$\alpha_{i\,i+1} = -a_{12}\frac{a_{23}}{a_{21}} \cdots \frac{a_{i\,i+1}}{a_{i\,i-1}} \qquad (i = 1,2,\ldots,n-1) \quad .$$

By setting

$$\alpha_{ii} = 0 \qquad (i = 1,2,\ldots,n)$$

$$\alpha_{ij} = 0 \qquad (\text{for } i+1 < j;\ i,j = 1,2,\ldots,n)$$

and

$$\alpha_{ij} = -\alpha_{ji} \qquad (i,j = 1,2,\ldots,n)$$

we have the desired result. □

Suppose there exists a positive equilibrium $x^* = (x_1^*, x_2^*, \ldots, x_n^*)$ for (4.2.1), hence also for (4.1.1). Define

$$V(x_1,x_2,\ldots,x_n) = \sum_{i=1}^{n} \beta_i \left(x_i - x_i^* - x_i^* \ln \frac{x_i}{x_i^*}\right)$$

(for $x_1,x_2,\ldots,x_n > 0$).

Lemma 4.2.2: (i) $V(x^*) = 0$ and

$$V(x) > 0 \quad \text{for} \quad x \neq x^*$$

(ii) The trajectory derivative V' of V along (4.2.1) is given by

$$V'(x_1,x_2,\ldots,x_n) = -\sum_{i=1}^{n} \lambda_i \beta_i (x_i - x_i^*)^2$$

(iii) $V(x) \to \infty$ as x tends to any of the invariant hyperplanes H_i $(i = 1,2,\ldots,n)$ or as $||x|| \to \infty$.

Proof: Consider the function $f : (0,\infty) \to R$ defined by

$$f(x) = x - a - a \ln \frac{x}{a} \qquad (x > 0)$$

where $a > 0$ is fixed.

Clearly, $f(a) = 0$

$$f'(x) = 1 - \frac{a}{x}$$

and

$$f''(x) = \frac{a}{x^2} \quad .$$

Now

$$f'(x) = 0 \Longrightarrow x = a$$

and

$$f''(a) > 0 \quad .$$

Therefore, f attains its minimum at $x = a$; and (i) then follows. For (ii),

$$V'(x_1,x_2,\ldots,x_n) = \sum_{i=1}^{n} \frac{\partial V}{\partial x_i} \dot{x}_i$$

$$= \sum_{i=1}^{n} \beta_i \left(1 - x_i^* \frac{1}{x_i} \frac{1}{x_i^*}\right) x_i \left(\epsilon_i - \lambda_i x_i + \frac{1}{\beta_i} \sum_{j=1}^{n} \alpha_{ij} x_j\right)$$

$$= \sum_{i=1}^{n} \beta_i (x_i - x_i^*)\left(\epsilon_i - \lambda_i x_i + \frac{1}{\beta_i} \sum_{j=1}^{n} \alpha_{ij} x_j\right) \quad .$$

Now since

$$\epsilon_i - \lambda_i x_i^* + \frac{1}{\beta_i} \sum_{j=1}^{n} \alpha_{ij} x_j^* = 0$$

therefore

$$V'(x_1,x_2,\ldots,x_n) = \sum_{i=1}^{n} \beta_i (x_i - x_i^*)\left(\lambda_i x_i^* - \frac{1}{\beta_i} \sum_{j=1}^{n} \alpha_{ij} x_j^* - \lambda_i x_i + \frac{1}{\beta_i} \sum_{j=1}^{n} \alpha_{ij} x_j\right)$$

$$= \sum_{i=1}^{n} \beta_i (x_i - x_i^*)\left[-\lambda_i (x_i - x_i^*) + \frac{1}{\beta_i} \sum_{j=1}^{n} \alpha_{ij} (x_j - x_j^*)\right]$$

$$= -\sum_{i=1}^{n} \lambda_i \beta_i (x_i - x_i^*)^2 + \sum_{i=1}^{n} \sum_{j=1}^{n} (x_i - x_i^*)\, \alpha_{ij} (x_j - x_j^*)$$

$$= -\sum_{i=1}^{n} \lambda_i \beta_i (x_i - x_i^*)^2 \quad ,$$

because $[\alpha_{ij}]$ is anti-symmetric.

(iii) is clear. □

Theorem 4.2.3: If a positive equilibrium x^* exists for (4.1.1), then

(i) x^* is stable,

(ii) solutions for system (4.1.1) with initial condition $\in \text{Int}(R_+^n)$ are bounded,

(iii) system (4.1.1) survives.

Proof: (ii) and (iii) follow from Lemma 4.2.2. (i) follows from Lemma 4.2.2 and Hale [33], p. 293, Theorem 1.1. □

Theorem 4.2.4: Suppose there exists a positive equilibrium x^* for (4.1.1) with $a_{11}, a_{22}, \ldots, a_{nn} < 0$, then

(i) x^* is globally asymptotically stable (over $\text{Int}(R_+^n)$)

(ii) the variational matrix M of (4.1.1) at x^* is qualitatively stable.

Proof: (i) follows immediately from Lemma 4.2.2 and Hale [33], p. 297, Corollary 1.2. For (ii), observe that

$$M = \begin{bmatrix} m_{11} & m_{12} & & & & & \\ m_{21} & m_{22} & m_{23} & & & & \\ & m_{32} & m_{33} & m_{34} & & & \\ & & & \ddots & & & \\ & & & & m_{n-1\,n-2} & m_{n-1\,n-1} & m_{n-1\,n} \\ & & & & & m_{n\,n-1} & m_{nn} \end{bmatrix}$$

where

$$m_{11} = a_{10} - 2a_{11}x_1^* - a_{12}x_2^* = -a_{11}x_1^* < 0$$

$$m_{12} = -a_{12}x_1^* < 0$$

$$m_{21} = a_{21}x_2^* > 0$$

$$m_{22} = -a_{20} + a_{21}x_1^* - 2a_{22}x_2^* - a_{23}x_3^* = -a_{22}x_2^* < 0$$

$$m_{23} = -a_{23}x_2^* < 0$$

$$\vdots$$

$$m_{n\,n-1} = a_{n\,n-1}x_n^* > 0$$

$$m_{n\,n} = -a_{n0} + a_{n\,n-1}x_{n-1}^* - 2a_{n\,n}x_n^* = -a_{n\,n}x_n^* < 0 .$$

Therefore by Theorem 2.2.1 and the remark following it, M is qualitatively stable. □

Remark: Using determinants, one can write down conditions for (4.1.1) to have a positive equilibrium.

§4.3 Persistence and Survivability

In this section, we shall consider the particular case of (4.1.1) when $a_{22} = \ldots = a_{nn} = 0$, i.e.,

$$(4.3.1)\qquad \begin{cases} x_1' = x_1 (a_{10} - a_{11} x_1 - a_{12} x_2) \\ x_2' = x_2 (-a_{20} + a_{21} x_1 - a_{23} x_3) \\ x_3' = x_3 (-a_{30} + a_{32} x_2 - a_{34} x_2) \\ \quad \cdot \\ \quad \cdot \\ \quad \cdot \\ x_{n-1}' = x_{n-1} (-a_{n-1\,0} + a_{n-1\,n-2} x_{n-2} - a_{n-1\,n} x_n) \\ x_n' = x_n (-a_{n\,0} + a_{n\,n-1} x_{n-1}) \end{cases}.$$

Theorem 4.3.1:

(i) Let $a_{11} = 0$ in (4.3.1) and n be even ($n = 2m+2$, say). Then there exists a positive equilibrium x^* for (4.3.1) iff $\mu_0 > 0$, where

$$\mu_0 = a_{10} - \sum_{i=1}^{m} a_{2i+1\,0} \prod_{j=1}^{i} \frac{a_{2j-1\,2j}}{a_{2j+1\,2j}} .$$

(ii) Let $a_{11} > 0$ in (4.3.1). Then there exists a positive equilibrium x^* for (4.3.1) iff $\mu > 0$, where

$$\mu = a_{10} - \sum_{i=1}^{m} a_{2i\,0} \prod_{j=1}^{i} \frac{a_{2j-2\,2j-1}}{a_{2j\,2j-1}} - \sum_{i=1}^{m} a_{2i+1\,0} \prod_{j=1}^{i} \frac{a_{2j-1\,2j}}{a_{2j+1\,2j}}$$

with

$$m = \begin{cases} \frac{n}{2} & \text{if } n \text{ is even} \\ \frac{n-1}{2} & \text{if } n \text{ is odd} \end{cases}$$

$$a_{01} \equiv a_{11} \quad \text{and} \quad a_{2m+1\,0} \equiv 0 \quad \text{if} \quad n = 2m \ .$$

(iii) The positive equilibrium x^* in(i) and (ii), if it exists, is unique.

Proof: The proof of (ii), which is similar to that of (i), will be given in §4.4. (iii) follows from the proofs of (i) and (ii). Consider (i). $x^* = (x_1^*, x_2^*, \ldots, x_n^*)$ is a positive equilibrium for (4.3.1) iff $x_i^* > 0 \quad (i = 1,2,\ldots,n)$, and

$$(4.3.2) \qquad \begin{cases} a_{10} - a_{12}\, x_2^* = 0 \\ -a_{20} + a_{21}\, x_1^* - a_{23}\, x_3^* = 0 \\ -a_{30} + a_{32}\, x_2^* - a_{34}\, x_4^* = 0 \\ \quad \cdot \\ \quad \cdot \\ \quad \cdot \\ -a_{n-1\,0} + a_{n-1\,n-2}\, x_{n-2}^* - a_{n-1\,n}\, x_n^* = 0 \\ -a_{n\,0} + a_{n\,n-1}\, x_{n-1}^* = 0 \ . \end{cases}$$

Clearly, we can determine the x_i^*'s from (4.3.2) in the order

$$x_{n-1}^* \to x_{n-3}^* \to \ldots \to x_1^*$$

and

$$x_2^* \to x_4^* \to \ldots \to x_n^*$$

(since n is even.) Now

$$x_{n-1}^* = \frac{a_{n0}}{a_{n\,n-1}}$$

$$x_{n-3}^* = \frac{a_{n-2\,0}}{a_{n-2\,n-3}} + \frac{a_{n-2\,n-1}}{a_{n-2\,n-3}}\, x_{n-1}^*$$

$$\cdot$$

$$\cdot$$

$$\cdot$$

$$x_1^* = \frac{a_{20}}{a_{21}} + \frac{a_{23}}{a_{21}}\, x_3^*$$

so that all $x_1^*, x_3, \ldots, x_{n-1}^*$ are > 0. On the other hand

$$x_{n-2}^* = \frac{a_{n-1\ 0}}{a_{n-1\ n-2}} + \frac{a_{n-1\ n}}{a_{n-1\ n-2}} x_n^*$$

$$\vdots$$

$$x_2^* = \frac{a_{30}}{a_{32}} + \frac{a_{34}}{a_{32}} x_4^*$$

so that all $x_2^*, \ldots, x_{n-2}^*, x_n^*$ are > 0 iff $x_n^* > 0$. Thus x^* exists iff $x_n^* > 0$. To calculate x_n^*, we note that

$$x_2^* = \frac{a_{10}}{a_{12}}$$

$$x_4^* = -\frac{a_{30}}{a_{34}} + \frac{a_{32}}{a_{34}} x_2^*$$

$$= -\frac{a_{30}}{a_{34}} + \frac{a_{10}}{a_{12}} \frac{a_{32}}{a_{34}}$$

$$x_6^* = -\frac{a_{50}}{a_{56}} + \frac{a_{54}}{a_{56}} x_4^*$$

$$= -\frac{a_{50}}{a_{34}} - \frac{a_{30}}{a_{34}} \frac{a_{54}}{a_{56}} + \frac{a_{10}}{a_{12}} \frac{a_{32}}{a_{34}} \frac{a_{54}}{a_{56}}$$

$$\vdots$$

$$x_n^* = -\frac{a_{n-1\ 0}}{a_{n-1\ n}} + \frac{a_{n-1\ n-2}}{a_{n-1\ n}} x_{n-2}^*$$

$$= -\frac{a_{n-1\ 0}}{a_{n-1\ n}} - \frac{a_{n-3\ 0}}{a_{n-1\ n}} \frac{a_{n-1\ n-2}}{a_{n-1\ n}} - \ldots - \frac{a_{30}}{a_{34}} \frac{a_{54}}{a_{56}} \cdots \frac{a_{n-1\ n-2}}{a_{n-1\ n}}$$

$$+ \frac{a_{10}}{a_{12}} \frac{a_{32}}{a_{34}} \cdots \frac{a_{n-1\ n-2}}{a_{n-1\ n}}$$

$$= \frac{1}{a_{12}} \frac{a_{32}}{a_{34}} \cdots \frac{a_{n-1\ n-2}}{a_{n-1\ n}} [-a_{n-1\ 0} \frac{a_{12}}{a_{22}} \frac{a_{34}}{a_{54}} \cdots \frac{a_{n-3\ n-2}}{a_{n-1\ n-2}}$$

$$- a_{n-3\ 0} \frac{a_{12}}{a_{32}} \frac{a_{34}}{a_{54}} \cdots \frac{a_{n-5\ n-4}}{a_{n-3\ n-4}} - \cdots - a_{30} \frac{a_{12}}{a_{32}} + a_{10}]$$

$$= \frac{1}{a_{12}} \frac{a_{32}}{a_{34}} \cdots \frac{a_{n-1\ n-2}}{a_{n-1\ n}} [a_{10} - \sum_{i=1}^{m} a_{2i+1\ 0} \prod_{j=1}^{j} \frac{a_{2j-1\ 2j}}{a_{2j+1\ 2j}}]$$

$$= \frac{1}{a_{12}} \frac{a_{32}}{a_{34}} \cdots \frac{a_{n-1\ n-2}}{a_{n-1\ n}} \mu_0 \cdot \square$$

Corollary 4.3.2: Let n be even in (4.3.1) with $a_{11} = 0$. If $\mu_0 > 0$, then

(i) a positive equilibrium x^* of (4.3.1) exists, is unique and is stable,

(ii) every solution of (4.3.1) with initial condition $\in$ Int (R_+^n) is bounded,

(iii) system (4.3.1) survives,

(iv) each of the hypersurfaces

$$V_c = \{x \in \text{Int } (R_+^n) : V(x) = c\} \quad \text{where} \quad c \geq 0$$

contains a recurrent motion for (4.3.1).

Proof: (i), (ii) and (iii) follow from Theorem 4.2.3 and Theorem 4.3.1. Since $a_{11} = a_{22} = \cdots = a_{n\ n} = 0$, by Lemma 4.2.2, $V' = 0$, so that V_c is a non-empty compact invariant set for (4.3.1). (iv) then follows from a classical theorem of Birkhoff (see Nemytskii and Stepanov [34], p. 374, Theorem 7.02 and p. 375, Theorem 7.06.) $\square$

Remark: The variational matrix of (4.3.1) at x^* with $a_{11} = 0$ is

of the form

$$M = \begin{bmatrix} 0 & m_{12} & & & & & \\ m_{21} & 0 & m_{23} & & & & \\ & m_{32} & \cdot & & & & \\ & & \cdot & \cdot & \cdot & \cdot & \\ & & \cdot & \cdot & \cdot & \cdot & \\ & & \cdot & \cdot & \cdot & \cdot & \\ & & & & & \cdot & \cdot \\ & & & & & \cdot & m_{n-1\,n} \\ & & & & & m_{n\,n-1} & 0 \end{bmatrix}$$

By the same transformation as in the alternate proof of Corollary 2.2.2, M can be transformated into the Schwarz matrix

$$\begin{bmatrix} 0 & -m_{n-1\,n}\, m_{n\,n-1} & & & & & \\ -1 & 0 & & & & & \\ & & \cdot & \cdot & \cdot & & \\ & & \cdot & \cdot & \cdot & & \\ & & \cdot & \cdot & \cdot & & \\ & & & & & \cdot & \cdot \\ & & & & & \cdot & -m_{12}m_{21} \\ & & & & & -1 & 0 \end{bmatrix}$$

Therefore all the eigenvalues of M are pure imaginary.

Corollary 4.3.3: Let $a_{11} > 0$ in (4.3.1).

(i) every solution of (4.3.1) with initial condition ϵR_+^n is

bounded.

(ii) if $\mu > 0$, then

(a) a positive equilibrium of (4.3.1) exists, is unique and is asymptotically stable,

(b) (4.3.1) survives.

Proof: We have only to show x^* is asymptotically stable. The rest follows from Theorem 4.1.1, Theorem 4.2.3, and Theorem 4.3.1. Now the variational matrix of (4.3.1) at x^* is given by

$$M = \begin{bmatrix} m_{11} & m_{12} & & & & & & \\ m_{21} & 0 & m_{23} & & & & & \\ & m_{32} & 0 & m_{34} & & & & \\ & & & \ddots & & & & \\ & & & & \ddots & & & \\ & & & & & \ddots & & \\ & & & & & & m_{n-1\,n-2} & 0 & m_{n-1\,n} \\ & & & & & & & m_{n\,n-1} & 0 \end{bmatrix}$$

where

$$m_{11} = a_{10} - 2a_{11}x_1^* - a_{12}x_1^* = -a_{11}x_1^* < 0$$

$$m_{12} = -a_{12}x_1^* < 0$$

$$m_{21} = a_{21}x_2^* > 0$$

$$m_{23} = -a_{23}x_2^* < 0$$

.

.

.

$$m_{n-1\ n-2} = a_{n-1\ n-2}x_{n-1}^* > 0$$

$$m_{n-1\ n} = -a_{n-1\ n}\ x_{n-1}^* < 0$$

$$m_{n\ n-1} = a_{n\ n-1}x_n^* > 0\ .$$

Therefore Corollary 2.2.2 applies. □

Remark: Gard and Hallam [3] proved that when $a_{11} > 0$, (4.3.1) is non-persistent if $\mu < 0$. We shall show in §4.6 that (4.3.1) is non-persistent if $\mu \leq 0$. They have also proved that when $a_{11} = 0$ and n is even, then (4.3.1) is non-persistent if $\mu_0 < 0$. We now show that (4.3.1) is non-persistent even when $\mu_0 = 0$.

Theorem 4.3.4: Let n be even and $a_{11} = 0$ in (4.3.1). If $\mu_0 = 0$, then (4.3.1) is non-persistent.

Proof: Let

$$\overline{x_2} = \frac{a_{10}}{a_{12}}$$

$$\overline{x_4} = -\frac{a_{30}}{a_{34}} + \frac{a_{32}}{a_{34}}\,\overline{x_2}$$

$$\vdots$$

$$\overline{\overline{x_{n-2}}} = -\frac{a_{n-3\ 0}}{a_{n-3\ n-2}} + \frac{a_{n-1\ n-2}}{a_{n-3\ n-2}}\,\overline{\overline{x_{n-2}}}$$

$$\overline{x_n} = -\frac{a_{n-1\ 0}}{a_{n-1\ n}} + \frac{a_{n-1\ n-2}}{a_{n-1\ n}}\,\overline{\overline{x_{n-2}}}\ .$$

Then $\overline{x_2}, \overline{x_4}, \ldots, \overline{\overline{x_{n-2}}} > 0$ and $\overline{x_n} = 0$ (c.f., proof of Theorem 4.3.1 (i)). Let also

$$\overline{\overline{x_{n-3}}} = \frac{a_{n-2\ 0}}{a_{n-2\ n-3}} + \frac{a_{n-2\ n-1}}{a_{n-2\ n-3}}\,\overline{\overline{x_{n-1}}}$$

$$\vdots$$

$$\overline{x_3} = \frac{a_{40}}{a_{43}} + \frac{a_{45}}{a_{43}}\,\overline{x_5}$$

$$\overline{x_1} = \frac{a_{20}}{a_{21}} + \frac{a_{23}}{a_{21}}\,\overline{x_3}\ .$$

Then $\overline{\overline{x_{n-1}}}, \overline{\overline{x_{n-3}}}, \ldots, \overline{x_3}, \overline{x_1} > 0$ provided $\overline{\overline{x_{n-1}}} > 0$. Clearly

$$L = \{\bar{x} = (\overline{x_1}, \overline{x_2}, \ldots, \overline{\overline{x_{n-1}}}, 0) : \overline{\overline{x_{n-1}}} > 0\}$$

is a line of equilibria of (4.3.1) in H_n.

The variational matrix of (4.3.1) at $\bar{x}$ is given by

$$
\begin{bmatrix}
0 & -a_{12}\overline{x_1} & & & & & & \\
a_{21}\overline{x_2} & 0 & -a_{23}\overline{x_2} & & & & & \\
 & a_{32}\overline{x_3} & \cdot & & & & & \\
 & & & \cdot\ \cdot\ \cdot\ \cdot & & & & \\
 & & & \cdot\ \cdot\ \cdot\ \cdot & & & & \\
 & & & \cdot\ \cdot\ \cdot\ \cdot & & & & \\
 & & & & & -a_{n-2\ n-1}\overline{x_{n-2}} & & \\
 & & & & a_{n-1\ n-2}\overline{x_{n-1}} & 0 & -a_{n-1\ n}\overline{x_{n-1}} & \\
 & & & & & 0 & -a_{n0}+a_{n\ n-1}\overline{x_{n-1}} &
\end{bmatrix}
$$

since $\overline{x_n} = 0$.

Now $-a_{n0} + a_{n\,n-1}\,\overline{x_{n-1}}$ is the eigenvalue of M in the x_n direction and it can be made < 0 if we choose $(0 <)\ x_{n-1} < \frac{a_{n0}}{a_{n\,n-1}}$. Therefore, for those points of L with $x_{n-1} < \frac{a_{n0}}{a_{n\,n-1}}$, each of them will have an asymptotically stable manifold intersecting Int (R^n_+). Hence (4.3.1) is non-persistent. □

Remark: In the case n is odd and $a_{11} = 0$, Gard and Hallam [3] showed that $\mu_0 > 0 \Longrightarrow$ (4.3.1) persistent and $\mu_0 < 0 \Longrightarrow$ (4.3.1) non-persistent where the definition of μ_0 is exactly the same as that given in Theorem 4.3.1, except that $m = \frac{n-1}{2}$.

For $\mu_0 = 0$, Freedman and Waltman [6] showed that when $n = 3$, every solution of (4.3.1) with intital condition $\in$ Int (R^3_+) is periodic, and hence (4.3.1) is persistent. The situation is unknown when n is arbitrary. However, it can be shown that when $\mu_0 = 0$, there is an infinite line of equilibria of (4.3.1) in Int (R^n_+) which is initiated from an equilibrium $\bar{x}$ of (4.3.1) in

$$\{x \in R^n_+ : x_1, x_2, \ldots, x_{n-1} > 0 \quad \text{and} \quad x_n = 0\}\ .$$

Random fluctuations can move the system from one equilibrium point to another. Eventually, these fluctuations will move the system to a neighborhood of $\bar{x}$, and x_n can be considered as extinct.

§4.4 Equilibria for (I_n)

In the following three sections, we shall be concerned with equation (4.3.1) with $a_{11} > 0$, i.e.,

$$(I_n)\quad \begin{cases} x_1' = x_1(a_{10} - a_{11}x_1 - a_{12}x_2) \\ x_2' = x_2(-a_{20} + a_{21}x_1 - a_{23}x_3) \\ x_3' = x_3(-a_{30} + a_{32}x_2 - a_{34}x_4) \\ \quad\vdots \\ x_{n-1}' = a_{n-1}(-a_{n-1\,0} + a_{n-1\,n-2}x_{n-2} - a_{n-1\,n}x_n) \\ x_n' = x_n(-a_{n0} + a_{n\,n-1}x_{n-1}) \end{cases}$$

where all the specified a_{ij} are > 0. Consider the system of equations

$$(4.4.1)\quad \begin{cases} x_1(a_{10} - a_{11}x_1 - a_{12}x_2) = 0 \\ x_2(-a_{20} + a_{21}x_1 - a_{23}x_3) = 0 \\ \quad\vdots \\ x_n(-a_{n0} + a_{n\,n-1}x_{n-1}) = 0 \end{cases}.$$

Since for $x_1, x_2, \ldots, x_n \geq 0$,

$$x_1 = 0 \Longrightarrow x_2 = 0 \Longrightarrow \ldots \Longrightarrow x_n = 0,$$

in (4.4.1), the only possible equilibria of (I_n) in R_+^n are of the form

$$\begin{cases} E_0^{(n)} = (0, 0, 0, \ldots, 0, 0) \\ E_1^{(n)} = (*, 0, 0, \ldots, 0, 0) \\ E_2^{(n)} = (*, *, 0, \ldots, 0, 0) \\ \quad \vdots \\ E_{n-1}^{(n)} = (*, *, *, \ldots, *, 0) \\ E_n^{(n)} = (*, *, *, \ldots, *, *) \end{cases}$$

where $*$ denotes a positive number. Of course, $E_n^{(n)}$ is the positive equilibrium of (I_n).

Our purpose in this section is to derive necessary and sufficient conditions for the existence of the equilibria

$$E_0^{(n)}, E_1^{(n)}, \ldots, E_n^{(n)} \quad \text{of} \quad (I_n)$$

and to see what are their coordinates if they exist.

Notation: For $x \in R_+^n$, let $p_i(x)$ denote the i^{th} coordinate of x. (This was denoted by x_i).

We separate into two cases.

Case 1: n is even, $n = 2m$ say.

Let $E_n^{(n)} \equiv x^* \equiv (x_1^*, \ldots, x_n^*) \equiv (x_1^*, \ldots, x_{2m}^*)$. Then since

$x_1^*, \ldots, x_{2m}^*$ are all > 0 and they satisfy

$$\begin{cases} a_{10} - a_{11}x_1 - a_{12}x_2 = 0 \\ -a_{20} + a_{21}x_1 - a_{23}x_3 = 0 \\ -a_{30} + a_{32}x_2 - a_{34}x_4 = 0 \\ \quad \cdot \\ \quad \cdot \\ \quad \cdot \\ -a_{2m-1\,0} + a_{2m-1\,2m-2}x_{2m-2} - a_{2m-1\,2m}x_{2m} = 0 \\ -a_{2m\,0} + a_{2m\,2m-1}x_{2m-1} = 0 \end{cases}$$

we can solve for them in the order

$$x^*_{2m-1} \to x^*_{2m-3} \to \cdots \to x^*_5 \to x^*_3 \to x^*_1 \to x^*_2 \to x^*_4$$
$$\to \cdots \to x^*_{2m-2} \to x^*_{2m} \ .$$

Using a computation similar to the proof of Theorem 4.3.1 (i) we see that

$x^*_1, x^*_3, \ldots, x^*_{2m-1}$ are all > 0

$x^*_2, x^*_4, \ldots, x^*_{2m-2}, x^*_{2m}$ will all > 0 iff $x^*_{2m} > 0$.

Moreover,

$$(4.4.2) \qquad p_{2k-1}(E_n^{(n)}) = x^*_{2k-1} = \sum_{i=k}^{m} \frac{a_{2i\,0}}{a_{2i\,2i-1}} \prod_{j=k}^{i-1} \frac{a_{2j\,2j+1}}{a_{2j\,2j-1}} \qquad (1 \le k \le m)$$

$$(4.4.3) \qquad p_2(E_n^{(n)}) = x^*_2 = \frac{a_{10}}{a_{12}} - \frac{a_{11}}{a_{12}} \sum_{i=1}^{m} \frac{a_{2i\,0}}{a_{2i\,2i-1}} \prod_{j=1}^{i-1} \frac{a_{2j\,2j+1}}{a_{2j\,2j-1}}$$

and

$$(4.4.4)\quad p_{2k}(E_n^{(n)}) = x_{2k}^* = \Big(\frac{1}{a_{12}} \prod_{i=2}^{k} \frac{a_{2i-1\ 2i-2}}{a_{2i-1\ 2i}} \Big) \cdot$$

$$\cdot \Big[a_{10} - \sum_{i=1}^{m} a_{2i\ 0} \prod_{j=1}^{i} \frac{a_{2j-2\ 2j-1}}{a_{2j\ 2j-1}}$$

$$- \sum_{i=1}^{k-1} a_{2i+1\ 0} \prod_{j=1}^{i} \frac{a_{2j-1\ 2j}}{a_{2j+1\ 2j}} \Big] \qquad (2 \le k \le m) .$$

Convention: $\sum_{\phi} = 0$, $\prod_{\phi} = 1$ (ϕ denotes the empty set).

Case 2: n is odd, $n = 2m+1$ say.

Let $E_n^{(n)} \equiv x^* \equiv (x_1^*, \ldots, x_{2m+1}^*)$.

Similar to Case 1, we obtain

$$(4.4.5)\quad p_{2k}(E_n^{(n)}) = \sum_{i=k}^{m} \frac{a_{2i+1\ 0}}{a_{2i+1\ 2i}} \prod_{j=k+1}^{i} \frac{a_{2j-1\ 2j}}{a_{2j-1\ 2j-2}} \qquad (1 \le k \le m)$$

$$(4.4.6)\quad p_1(E_n^{(n)}) = \frac{a_{10}}{a_{11}} - \frac{a_{12}}{a_{11}} \sum_{i=1}^{m} \frac{a_{2i-1\ 2i}}{a_{2i-1\ 2i-2}} \prod_{j=2}^{i} \frac{a_{2j-1\ 2j}}{a_{2j-1\ 2j-2}}$$

and

$$(4.4.7)\quad p_{2k+1}(E_n^{(n)}) = \frac{1}{a_{11}} \prod_{i=1}^{k} \frac{a_{2i\ 2i-1}}{a_{2i\ 2i+1}}$$

$$\Big[a_{10} - \sum_{i=1}^{m} a_{2i+1\ 0} \prod_{j=1}^{i} \frac{a_{2j-1\ 2j}}{a_{2j+1\ 2j}}$$

$$- \sum_{i=1}^{k} a_{2i\ 0} \prod_{j=1}^{i} \frac{a_{2j-2\ 2j-1}}{a_{2j\ 2j-1}} \Big] \qquad (1 \le k \le m) .$$

Proof of Theorem 4.3.1 (ii): As noted before,

$$E_n^{(n)} \quad \text{exists iff} \quad p_n(E_n^{(n)}) > 0$$

Now, for even n, by (4.4.4),

$$p_n(E_n^{(n)}) = \left(\frac{1}{a_{12}} \prod_{i=2}^{m} \frac{a_{2i-1\ 2i-2}}{a_{2i-1\ 2i}}\right)\left[a_{10} - \sum_{i=1}^{m} a_{2i\ 0} \prod_{j=1}^{i} \frac{a_{2j-2\ 2j-1}}{a_{2j\ 2j-1}}\right.$$

$$\left. - \sum_{i=1}^{m-1} a_{2i+1\ 0} \prod_{j=1}^{i} \frac{a_{2j-1\ 2j}}{a_{2j+1\ 2j}}\right] .$$

Since $a_{2m+1\ 0} = 0$, therefore

$$p_n(E_n^{(n)}) > 0 \quad \text{iff} \quad \mu > 0 .$$

The case when n is odd can be dealt with similarly using (4.4.7). □

Remarks: (i) By noting that

$$(4.4.8) \quad \begin{cases} p_i(E_{n-1}^{(n)}) = p_i(E_{n-1}^{(n-1)}) & \forall\ 1 \le i \le n-1 \\ p_i(E_{n-2}^{(n)}) = p_i(E_{n-2}^{(n)}) & \forall\ 1 \le i \le n-2 \\ \cdot \\ \cdot \\ \cdot \\ p_i(E_1^{(n)}) = p_i(E_1^{(1)}) & \text{for } i = 1 \end{cases}$$

we can calculate all the coordinates of

$$E_0^{(n)}, E_1^{(n)}, \ldots, E_{n-1}^{(n)} \quad \text{and} \quad E_n^{(n)} \quad (n = 1,2,\ldots)$$

using (4.4.2), (4.4.3), (4.4.4), (4.4.5), (4.4.6) and (4.4.7).

(ii) $E_0^{(n)}, E_1^{(n)}, \ldots,$ or $E_n^{(n)}$, if any exist, must be unique.

Notation: To avoid confusion, we shall denote μ (which is defined in §4.3 for (I_n)) by $\mu^{(n)}$ in the rest of this section and in §4.6.

Remarks: (i) For $2 \leq i \leq n$

$$E_i^{(n)} \text{ exists iff } E_i^{(i)} \text{ exists, i.e., iff } \mu^{(i)} > 0$$

(ii) $E_0^{(n)} = (0, 0, \ldots, 0)$

and

$$E_1^{(n)} = \left(\frac{a_{10}}{a_{11}}, 0, \ldots, 0\right)$$

always exist.

Theorem 4.4.1: There exist numbers

$$\overline{\mu_1^{(n)}}, \overline{\mu_2^{(n)}}, \ldots, \overline{\mu_{n-2}^{(n)}}, \overline{\mu_{n-1}^{(n)}}$$

with

$$\overline{\mu_1^{(n)}} < \overline{\mu_2^{(n)}} < \ldots < \overline{\mu_{n-2}^{(n)}} < \overline{\mu_{n-1}^{(n)}}$$

such that

(1) $\overline{\mu_{n-1}^{(n)}} < \mu^{(n)}$ iff $E_0^{(n)}, E_1^{(n)}, \ldots, E_{n-1}^{(n)}, E_n^{(n)}$ exist

(2) $\overline{\mu_{n-2}^{(n)}} < \overline{\mu^{(n)}} \leq \overline{\mu_{n-1}^{(n)}}$

iff $E_0^{(n)}, E_1^{(n)}, \ldots, E_{n-1}^{(n)}$ exist but not $E_n^{(n)}$

(3) $\overline{\mu_{n-3}^{(n)}} < \overline{\mu^{(n)}} \leq \overline{\mu_{n-2}^{(n)}}$

iff $E_0^{(n)}, E_1^{(n)}, \ldots, E_{n-2}^{(n)}$ exist but not $E_{n-1}^{(n)}, E_n^{(n)}$.

.
.
.

(n-1) $\overline{\mu_1^{(n)}} < \overline{\mu^{(n)}} \leq \overline{\mu_2^{(n)}}$

iff $E_0^{(n)}, E_1^{(n)}, E_2^{(n)}$ exist but not $E_3^{(n)}, \ldots, E_n^{(n)}$

(n) $-\infty < \mu^{(n)} \leq \overline{\mu_1^{(n)}}$

iff $E_0^{(n)}, E_1^{(n)}$ exist but not $E_2^{(n)}, \ldots, E_n^{(n)}$.

Proof: Case 1: n is even, $n = 2m$ say. Since

$$\mu^{(2m)} = a_{10} - \sum_{i=1}^{m} a_{2i\,0} \prod_{j=1}^{i} \frac{a_{2j-2\;2j-1}}{a_{2j\;2j-1}} - \sum_{i=1}^{m-1} a_{2i+1\,0} \prod_{j=1}^{i} \frac{a_{2j-1\;2j}}{a_{2j+1\;2j}}$$

$$\mu^{(2k)} = a_{10} - \sum_{i=1}^{m} a_{2i\,0} \prod_{j=1}^{i} \frac{a_{2j-2\;2j-1}}{a_{2j\;2j-1}} - \sum_{i=1}^{k-1} a_{2i+1\,0} \prod_{j=1}^{i} \frac{a_{2j-1\;2j}}{a_{2j+1\;2j}}$$

(for $1 \leq k \leq m-1$)

and

$$\mu^{(2k+1)} = a_{10} - \sum_{i=1}^{k} a_{2i\,0} \prod_{j=1}^{i} \frac{a_{2j-2\;2j-1}}{a_{2j\;2j-1}} - \sum_{i=1}^{k} a_{2i+1\,0} \prod_{j=1}^{i} \frac{a_{2j-1\;2j}}{a_{2j+1\;2j}}$$

(for $1 \leq k \leq m-1$) .

Therefore if we define

$$\overline{\mu_{2k-2}^{(2m)}} = -\left(\sum_{i=k}^{m} a_{2i\,0} \prod_{j=1}^{i} \frac{a_{2j-2\;2j-1}}{a_{2j\;2j-1}} + \sum_{i=}^{m-1} a_{2i+1\,0} \prod_{j=1}^{i} \frac{a_{2j-2\;2j-1}}{a_{2j\;2j-1}} \right)$$

(for $2 \leq k \leq m$)

$$\overline{\mu^{(2m)}_{2k-1}} = -\left(\sum_{i=k+1}^{m} a_{2i\ 0} \prod_{j=1}^{i} \frac{a_{2j-2\ 2j-1}}{a_{2j\ 2j-1}} + \sum_{i=k}^{m-1} a_{2i+1\ 0} \prod_{j=1}^{i} \frac{a_{2j+1\ 2j}}{a_{2j+1\ 2j}} \right)$$

(for $1 \leq k \leq m-1$)

and

$$\overline{\mu^{(2m)}_{2m-1}} = 0$$

then

$$\overline{\mu^{(2m)}_{1}} < \overline{\mu^{(2m)}_{2}} < \ldots < \overline{\mu^{(2m)}_{2m-1}} = 0$$

and

$$\overline{\mu^{(2m)}_{i}} < \mu^{(2m)} \quad \text{iff} \quad \mu^{(i+1)} > 0 \quad (1 \leq i \leq 2m-1) .$$

Hence the proof is complete for the case when n is even.

Case 2: n is odd, $n = 2m+1$ say. Define

$$\overline{\mu^{(2m+1)}_{2k}} = -\left(\sum_{i=k+1}^{m} a_{2i\ 0} \prod_{j=1}^{i} \frac{a_{2j-2\ 2j-1}}{a_{2j\ 2j-1}} + \sum_{i=k+1}^{m} a_{2i+1\ 0} \prod_{j=1}^{i} \frac{a_{2j-1\ 2j}}{a_{2j+1\ 2j}} \right)$$

(for $1 \leq k \leq m-1$)

$$\overline{\mu^{(2m+1)}_{2k-1}} = -\left(\sum_{i=k+1}^{m} a_{2i\ 0} \prod_{j=1}^{i} \frac{a_{2j-2\ 2j-1}}{a_{2j\ 2j-1}} + \sum_{i=k}^{m} a_{2i+1\ 0} \prod_{j=1}^{i} \frac{a_{2j-1\ 2j}}{a_{2j+1\ 2j}} \right)$$

(for $1 \leq k \leq m-1$)

and

$$\overline{\mu^{(2m+1)}_{2m}} = 0 .$$

Then, as is Case 1, we can show that

$$\overline{\mu^{(2m+1)}_{1}} < \overline{\mu^{(2m+1)}_{2}} < \ldots < \overline{\mu^{(2m+1)}_{2m+1}} = 0$$

and

$$\overline{\mu_i^{(2m+1)}} < \mu^{(2m+1)} \quad \text{iff} \quad \mu^{(i+1)} > 0$$

$(1 \leq i \leq 2m)$. □

§4.5 Alternating Equilibrium Numbers Phenomenon

Theorem 4.5.1: The following two diagrams hold

$$
(4.5.1)\quad \left\{\begin{array}{lllll}
P_1(E_0^{(n)}) = 0 & & & & \\
\wedge & & & & \\
P_1(E_1^{(n)}) & P_2(E_1^{(n)}) = 0 & & & \\
\vee \quad <=> & \wedge & & & \\
P_1(E_2^{(n)}) & P_2(E_2^{(n)}) & P_3(E_2^{(n)}) = 0 & & \\
\wedge \quad <=> & \vee \quad <=> & \wedge & & \\
P_1(E_3^{(n)}) & P_2(E_3^{(n)}) & P_3(E_3^{(n)}) & & \\
\vdots & & & & \\
P_1(E_{n-1}^{(n)}) & P_2(E_{n-1}^{(n)}) & P_3(E_{n-1}^{(n)}) & \cdots & P_n(E_{n-1}^{(n)}) = 0 \\
\vee \quad <=> & \wedge \quad <=> & \vee & & \vee \quad <=> \quad \wedge \\
P_1(E_n^{(n)}) & P_2(E_n^{(n)}) & P_3(E_n^{(n-1)}) & & P_n(E_n^{(n)})
\end{array}\right.
$$

if n is even,

and

$$
(4.5.2)\quad
\begin{cases}
P_1(E_n^{(n)}) = 0 \\
\quad \wedge \\
P_1(E_1^{(n)}) \quad P_2(E_1^{(n)}) = 0 \\
\quad \vee \quad <=> \quad \wedge \\
P_1(E_2^{(n)}) \quad P_2(E_2^{(n)}) \quad P_3(E_2^{(n)}) = 0 \\
\quad \wedge \quad <=> \quad \vee \quad <=> \quad \wedge \\
P_1(E_3^{(n)}) \quad P_2(E_3^{(n)}) \quad P_3(E_3^{(n)}) \\
\quad \cdot \\
\quad \cdot \\
\quad \cdot \\
P_1(E_{n-1}^{(n)}) \quad P_2(E_{n-1}^{(n)}) \quad P_3(E_{n-1}^{(n)}) \quad P_{n-1}(E_{n-1}^{(n)}) \quad P_n(E_{n-1}^{(n)}) = 0 \\
\quad \wedge \quad <=> \quad \vee \quad <=> \quad \wedge \quad \ldots \quad \vee \quad <=> \quad \wedge \\
P_1(E_n^{(n)}) \quad P_2(E_n^{(n)}) \quad P_3(E_n^{(n)}) \quad P_{n-1}(E_n^{(n)}) \quad P_n(E_n^{(n)})
\end{cases}
$$

if n is odd.

Note: $\vee$ <=> $\wedge$ or $\wedge$ <=> $\vee$ indicate that the inequalities are equivalent.

Remark: This phenomenon has been noted by Gard and Hallam [3] for $n = 4$.

Proof of Theorem: It suffices to show

$$
(4.5.3)\quad
\begin{array}{ccccccccccc}
P_1(E_{n-1}^{(n)}) & & P_2(E_{n-1}^{(n)}) & & P_3(E_{n-1}^{(n)}) & & P_{n-1}(E_{n-1}^{(n)}) & & P_n(E_{n-1}^{(n)}) \\
\vee & <=> & \wedge & <=> & \vee & \ldots & \vee & <=> & \wedge \\
P_1(E_n^{(n)}) & & P_2(E_n^{(n)}) & & P_3(E_n^{(n)}) & & P_{n-1}(E_n^{(n)}) & & P_n(E_n^{(n)})
\end{array}
$$

if n is even,

and

$$\begin{array}{ccccccccc} P_1(E_{n-1}^{(n)}) & & P_2(E_{n-1}^{(n)}) & & P_3(E_{n-1}^{(n)}) & & P_{n-1}(E_{n-1}^{(n)}) & & P_n(E_{n-1}^{(n)}) \\ \wedge & \Leftrightarrow & \vee & \Leftrightarrow & \wedge & \cdots & \vee & \Leftrightarrow & \wedge \\ P_1(E_n^{(n)}) & & P_2(E_n^{(n)}) & & P_3(E_n^{(n)}) & & P_{n-1}(E_n^{(n)}) & & P_n(E_n^{(n)}) \end{array} \tag{4.5.4}$$

if n is odd,

because the remaining equivalences of the two diagrams (4.5.1) and (4.5.2) follow directly from (4.5.3), (4.5.4) and (4.4.8)

Case 1: n is even, $n = 2m$ say.

We have to check the equivalence of the following three inequalities

(a) $P_n(E_n^{(n)}) > P_n(E_{n-1}^{(n)}) = 0$

(b) $P_{2k}(E_n^{(n)}) > P_{2k}(E_{n-1}^{(n)})$

$= P_{2k}(E_{n-1}^{(n-1)})$ by (4.4.8)

$(1 \leq k \leq m-1)$

and

(c) $P_{2k-1}(E_n^{(n)}) < P_{2k-1}(E_{n-1}^{(n)})$

$= P_{2k-1}(E_{n-1}^{(n-1)})$ by (4.4.8)

$(1 \leq k \leq m)$.

Now by (4.4.4), (a) becomes

$$\left(\frac{1}{a_{11}} \sum_{i=2}^{m} \frac{a_{2i-1\ 2i-2}}{a_{2i-1\ 2i}} \right) \left[a_{10} - \sum_{i=1}^{m} a_{2i\ 0} \prod_{j=1}^{i} \frac{a_{2j-2\ 2j-1}}{a_{2j\ 2j-1}} \right.$$

$$\left. - \sum_{i=1}^{m-1} a_{2i+1\ 0} \prod_{j=1}^{i} \frac{a_{2j-1\ 2j}}{a_{2j\ 2j-1}} \right] > 0$$

$$\text{i.e.,} \quad a_{10} > \sum_{i=1}^{m} a_{2i\ 0} \prod_{j=1}^{i} \frac{a_{2j-2\ 2j-1}}{a_{2j\ 2j-1}} + \sum_{i=1}^{m-1} a_{2i+1\ 0} \prod_{j=1}^{i} \frac{a_{2j-1\ 2j}}{a_{2j+1\ 2j}} \ .$$

By (4.4.4) and (4.4.5), (b) becomes

$$\left(\frac{1}{a_{12}} \prod_{i=2}^{k} \frac{a_{2i-1\ 2i-2}}{a_{2i-1\ 2i}} \right) \left[a_{10} - \sum_{i=1}^{m} a_{2i\ 0} \prod_{j=1}^{i} \frac{a_{2j-2\ 2j-1}}{a_{2j\ 2j-1}} \right.$$

$$\left. - \sum_{i=1}^{k-1} a_{2i+1\ 0} \prod_{j=1}^{i} \frac{a_{2j-1\ 2j}}{a_{2j+1\ 2j}} \right]$$

$$> \sum_{i=k}^{m-1} \frac{a_{2i+1\ 0}}{a_{2i+1\ 2i}} \prod_{j=k+1}^{i} \frac{a_{2j-1\ 2j}}{a_{2j-1\ 2j-2}} \ .$$

By noting that

$$\frac{1}{\frac{1}{a_{12}} \prod_{i=2}^{k} \frac{a_{2i-1\ 2i-2}}{a_{2i-1\ 2i}}} \sum_{i=k}^{m-1} \frac{a_{2i+1\ 0}}{a_{2i+1\ 2i}} \prod_{j=k+1}^{i} \frac{a_{2j-1\ 2j}}{a_{2j-1\ 2j-2}}$$

$$= \sum_{i=k}^{m-1} a_{2i+1\ 0} \prod_{j=1}^{i} \frac{a_{2j-1\ 2j}}{a_{2j+1\ 2j}} \ ,$$

the equivalence of (a) and (b) is then evident.

On the other hand, by (4.4.2) and (4.4.7), (c) becomes

$$(4.5.5)\qquad \sum_{i=k}^{m} \frac{a_{2i\,0}}{a_{2i\,2i-1}} \prod_{j=k}^{i-1} \frac{a_{2j\,2j+1}}{a_{2j\,2j-1}}$$

$$< \frac{1}{a_{11}} \prod_{i=1}^{k-1} \frac{a_{2i\,2i-1}}{a_{2i\,2i+1}} \Big[a_{10} - \sum_{i=1}^{m-1} a_{2i+1\,0} \prod_{j=1}^{i} \frac{a_{2j-1\,2j}}{a_{2j+1\,2j}}$$

$$- \sum_{i=1}^{k-1} a_{2i\,0} \prod_{j=1}^{i} \frac{a_{2j-2\,2j-1}}{a_{2j\,2j-1}} \Big]$$

for $2 \leq k \leq m$

and by (4.4.2) and (4.4.6), (c) becomes

$$(4.5.6)\qquad \sum_{i=1}^{m} \frac{a_{2i\,0}}{a_{2i\,2i-1}} \prod_{j=1}^{i-1} \frac{a_{2j\,2j+1}}{a_{2j\,2j-1}}$$

$$< \frac{a_{10}}{a_{11}} - \frac{a_{12}}{a_{11}} \sum_{i=1}^{m-1} \frac{a_{2i+1\,0}}{a_{2i+1\,2i}} \prod_{j=2}^{i} \frac{a_{2j-1\,2j}}{a_{2j-1\,2j-2}}$$

for $k = 1$.

By noting

$$\frac{1}{\frac{1}{a_{11}} \prod_{i=1}^{k-1} \frac{a_{2i\,2i-1}}{a_{2i\,2i+1}}} \sum_{i=k}^{m} \frac{a_{2i\,0}}{a_{2i\,2i-1}} \prod_{j=k}^{i-1} \frac{a_{2j\,2j+1}}{a_{2j\,2j-1}}$$

$$= \sum_{i=k}^{m} a_{2i\,0} \prod_{j=1}^{i} \frac{a_{2j-2\,2j-1}}{a_{2j\,2j-1}}$$

in (4.5.5), and

$$a_{12} \sum_{i=1}^{m-1} \frac{a_{2i+1\ 0}}{a_{2i+1\ 2i}} \prod_{j=2}^{i} \frac{a_{2j-1\ 2j}}{a_{2j-1\ 2j-2}} = \sum_{i=1}^{m-1} a_{2i+1\ 0} \prod_{j=1}^{i} \frac{a_{2j-1\ 2j}}{a_{2j+1\ 2j}}$$

and

$$a_{11} \sum_{i=1}^{m} \frac{a_{2i\ 0}}{a_{2i\ 2i-1}} \prod_{j=1}^{i-1} \frac{a_{2j\ 2j+1}}{a_{2j\ 2j-1}} = \sum_{i=1}^{m} a_{2i\ 0} \prod_{j=1}^{i} \frac{a_{2j-2\ 2j-1}}{a_{2j\ 2j-1}}$$

in (4.5.6), the equivalence of (a) and (c) becomes evident.

Case 2: n is odd, $n = 2m+1$ say.

We ha e to show that the following three inequalities are equivalent,

(d) $p_n(E_n^{(n)}) > p_n(E_{n-1}^{(n)}) = 0$

(e) $p_{2k}(E_n^{(n)}) < p_{2k}(E_{n-1}^{(n)})$

$= p_{2k}(E_{n-1}^{(n-1)})$ by (4.4.8)

$(1 \leq k \leq m)$

(f) $p_{2k+1}(E_n^{(n)}) > p_{2k+1}(E_{n-1}^{(n)})$

$= p_{2k+1}(E_{n-1}^{(n-1)})$ by (4.4.8)

$(0 \leq k \leq m)$.

Since the proof of the equivalence of (d), (e) and (f) is similar to that of Case 1 (using (4.4.2)-(4.4.7)), we shall omit the details in here. □

§4.6 Global Stability

In this section, we shall give a complete classification of the flow of (I_n). More precisely, we shall show that by decreasing the value of the parameter $\mu = \mu^{(n)}$, the equilibria

$$E_n^{(n)}, \ E_{n-1}^{(n)}, \ \ldots, \ E_1^{(n)}$$

will in turn become globally stable. But before we state and prove this theorem, let us consider (I_1) and (I_2) to gain more insight into the general case (I_n).

(i) $n = 1$: Then (I_n) becomes

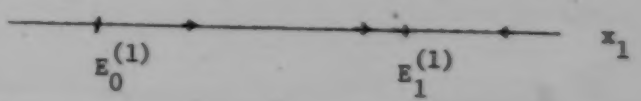
$$(I_1) \qquad x_1' = x_1(a_{10} - a_{11}x_1) \ .$$

Clearly

$$p_1(E_0^{(1)}) = 0$$

$$p_1(E_1^{(1)}) = \frac{a_{10}}{a_{11}}$$

and the phase portrait of (I_1) looks like



Therefore $E_1^{(1)}$ is globally stable (over Int (R_+)) .

(ii) $n = 2$: (I_n) becomes

$$(I_2) \quad \begin{cases} x_1' = x_1(a_{10} - a_{11}x_1 - a_{12}x_2) & (\equiv f_1(x_1,x_2)) \\ x_2' = x_2(-a_{20} + a_{21}x_1) & (\equiv f_2(x_1,x_2)) \end{cases}$$

Clearly,

$$E_0^{(2)} = (0, 0)$$

$$E_1^{(2)} = (\frac{a_{10}}{a_{11}}, 0)$$

and

$$E_2^{(2)} = (\frac{a_{20}}{a_{21}}, \frac{a_{10}}{a_{12}} - \frac{a_{11}}{a_{12}}\frac{a_{20}}{a_{21}}) .$$

Note that $E_2^{(2)}$ exists iff $\frac{a_{10}}{a_{11}} > \frac{a_{20}}{a_{21}}$.

Case 1: $E_2^{(2)}$ does not exist, i.e., $\frac{a_{10}}{a_{11}} \leq \frac{a_{20}}{a_{21}}$.

By Coddington and Levinson [35], p. 400, Corollary 1, there can be no periodic solution for (I_2) in Int R_+^2, hence no periodic solution for (I_2) in R_+^2. Now the variational matrix of (I_2) is

$$M = \begin{bmatrix} a_{10}-2a_{11}x_1-a_{12}x_2 & -a_{12}x_1 \\ a_{21}x_2 & -a_{20}+a_{21}x_1 \end{bmatrix} .$$

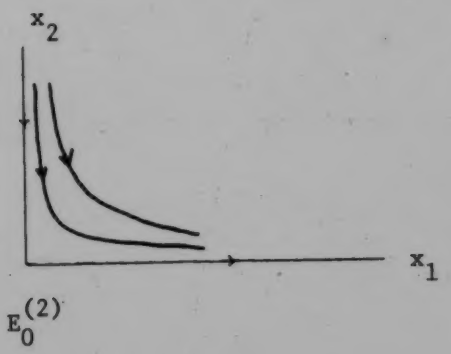
At $E_0^{(2)}$

$$M = \begin{bmatrix} a_{10} & 0 \\ 0 & -a_{20} \end{bmatrix} .$$

At $E_1^{(2)}$

$$M = \begin{bmatrix} -a_{11} & -\frac{a_{10}\,a_{12}}{a_{11}} \\ 0 & -a_{20} + \frac{a_{10}\,a_{21}}{a_{11}} \end{bmatrix} .$$

Since $E_0^{(2)}$ is a hyperbolic point whose neighboring flow looks like



then by boundedness of solutions and the Poincare-Bendixson theorem (see Coddington and Levinson [34], p. 391), $E_1^{(2)}$ is globally stable (over Int (R_+^2)).

Case 2: $E_2^{(2)}$ exists, i.e., $\frac{a_{10}}{a_{11}} > \frac{a_{20}}{a_{21}}$. Let $B(x_1,x_2) = \frac{1}{x_1x_2}$. Then

$$\frac{\partial(Bf_1)}{\partial x_1} = -\frac{a_{11}}{x_2}$$

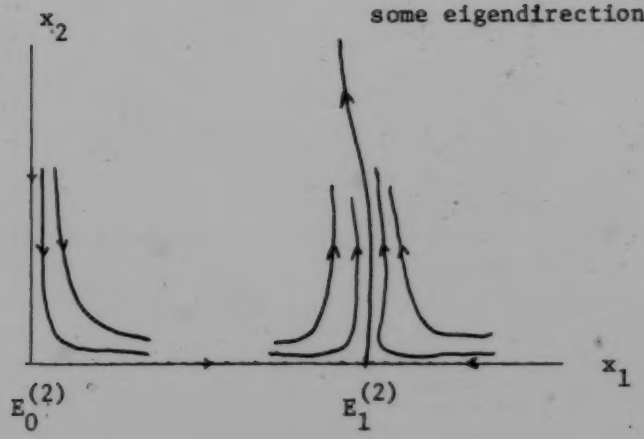
and

$$\frac{\partial(Bf_2)}{\partial x_2} = 0$$

so that

$$\frac{\partial(Bf_1)}{\partial x_1} + \frac{\partial(Bf_2)}{\partial x_2} < 0 \quad \text{on Int } (R_+^2) .$$

Hence by Dulac's criterion (§1.2 (1)) there can be no periodic solution of (I_2) in Int R_+^2. Moreover, in this case, both $E_0^{(2)}$ and $E_1^{(2)}$ are hyperbolic points whose neighboring flows look like



therefore, again by the Poincare-Bendixson therorem, $E_2^{(2)}$ is globally stable.

Theorem 4.6.1: Let $\overline{\mu_n^{(n)}} = \infty$ and $\overline{\mu_0^{(n)}} = -\infty$. Then

$$\overline{\mu_k^{(n)}} < \mu^{(n)} \leq \overline{\mu_{k+1}^{(n)}} \Longrightarrow E_{k+1}^{(n)} \quad \text{is globally stable}$$

$$(0 \leq k \leq n-1) .$$

Proof: (i) $k = n-1$. Then $E_n^{(n)}$ exists, let $E_n^{(n)} = (x_1^*, \ldots, x_n^*)$ and define V as in §4.2.

By Lemma 4.2.2, the set

$$M = \{x \in \text{Int } R_+^n : x_1 = x_1^* \}$$

is such that

$$V' < 0 \qquad \text{outside } M$$

$$V' = 0 \qquad \text{on } M .$$

Therefore to show that x^* is globally stable, by the theorem of Barbaskin and Krasovskii stated in §1.2 (5), it suffices to show M

contains no entire trajectories of (I_n) except $E_n^{(n)}$. Now suppose $x(t) = (x_1(t), \ldots, x_n(t))$ is a solution of (I_n) such that

$$x(t) \in M \qquad \forall\, t \geq 0 \ .$$

Then

$$x_1(t) = x_1^*$$

$$\Longrightarrow \quad x_1'(t) = 0$$

$$\Longrightarrow \quad x_2(t) = x_2^* \qquad \text{by the } 1^{st} \text{ equation of } (I_n)$$

$$\Longrightarrow \quad x_2'(t) = 0$$

$$\Longrightarrow \quad x_3(t) = x_3^* \qquad \text{by the } 2^{nd} \text{ equation of } (I_n)$$

etc.

Hence we must have $x(t) = E_n^{(n)} \quad \forall\, t \geq 0$

(ii) Suppose $\overline{\mu_k^{(n)}} < \mu^{(n)} \leq \overline{\mu_{k+1}^{(n)}} \qquad (0 \leq k \leq n-2)$. By Theorem 4.4.1,

$$E_0^{(n)}, E_1^{(n)}, \ldots, E_{k+1}^{(n)} \quad \text{exist}$$

but not

$$E_{k+2}^{(n)}, \ldots, E_n^{(n)} \ .$$

Define the function

$$W : B_{k+1} \to R$$

where

$$B_{k+1} = \{x \in R_+^n : x_i \geq 0 \qquad (k+2 \leq i \leq n) \quad \text{and}$$

$$x_i > 0 \qquad (i \leq i \leq k+1)\}$$

as follows:

$$W(x_1,\ldots,x_n) = \sum_{i=1}^{k+1} \beta_i [x_i - p_i(E_{k+1}^{(n)}) - p_i(E_{k+1}^{(n)}) \ln \frac{x_i}{p_i(E_{k+1}^{(n)})}]$$

$$+ \sum_{i=k+2}^{n} \beta_i x_i \quad .$$

Then

$$W'(x_1,\ldots,x_n)$$

$$= \sum_{i=1}^{k+1} \beta_i \left[1 - p_i(E_{k+1}^{(n)}) \frac{1}{\frac{x_i}{p_i(E_{k+1}^{(n)})}} \frac{1}{p_i(E_{k+1}^{(n)})}\right] x_i'$$

$$+ \sum_{i=k+2}^{n} \beta_i x_i'$$

$$= \sum_{i=1}^{k+1} \beta_i (x_i - p_i(E_{k+1}^{(n)}))(\epsilon_i - \lambda_i x_i + \frac{1}{\beta_i} \sum_{j=1}^{n} \alpha_{ij} x_j)$$

$$+ \sum_{i=k+2}^{n} \beta_i x_i (\epsilon_i - \lambda_i x_i + \frac{1}{\beta_i} \sum_{j=1}^{n} \alpha_{ij} x_j)$$

$$= \sum_{i=1}^{k+1} \beta_i (x_i - p_i(E_{k+1}^{(n)}))[-\lambda_i (x_i - p_i(E_{k+1}^{(n)}))$$

$$+ \frac{1}{\beta_i} \sum_{j=1}^{n} \alpha_{ij} (x_j - p_j(E_{k+1}^{(n)}))]$$

$$+ \sum_{i=k+1}^{n} \beta_i x_i (\epsilon_i + \frac{1}{\beta_i} \sum_{j=1}^{n} \alpha_{ij} x_j) \quad ,$$

since

$$\epsilon_i - \lambda_i p_i(E_{k+1}^{(n)}) + \frac{1}{\beta_i} \sum_{j=1}^{n} \alpha_{ij} p_j(E_{k+1}^{(n)}) = 0$$

$$(\text{for} \quad 1 \leq i \leq k+1)$$

and $\lambda_i = 0$ (for $2 \le i \le n$)

$$= - \sum_{i=1}^{k+1} \lambda_i \beta_i (x_i - p_i(E_{k+1}^{(n)}))^2$$

$$+ \sum_{i=1}^{k+1} \sum_{j=1}^{n} (x_i - p_i(E_{k+1}^{(n)})) \alpha_{ij} (x_j - p_j(E_{k+1}^{(n)}))$$

$$+ \sum_{i=k+2}^{n} \epsilon_i \beta_i x_i + \sum_{i=k+2}^{n} \sum_{j=1}^{n} x_i \alpha_{ij} x_j$$

$$= - \lambda_1 \beta_1 (x_1 - p_1(E_{k+1}^{(n)}))^2$$

$$+ \sum_{i=1}^{k+1} \sum_{j=1}^{k+1} (x_i - p_i(E_{k+1}^{(n)})) \alpha_{ij} (x_j - p_j(E_{k+1}^{(n)}))$$

$$+ \sum_{i=1}^{k+1} \sum_{j=k+2}^{n} (x_i - p_i(E_{k+1}^{(n)})) \alpha_{ij} (x_j - p_j(E_{k+1}^{(n)}))$$

$$+ \sum_{i=k+2}^{n} \epsilon_i \beta_i x_i + \sum_{i=k+2}^{n} \sum_{j=k+2}^{n} x_i \alpha_{ij} x_j$$

$$+ \sum_{i=k+2}^{n} \sum_{j=1}^{k+1} x_i \alpha_{ij} x_j ,$$

since $\lambda_i = 0$ $(2 \le i \le n)$

$$= -\lambda_1 \beta_1 (x_1 - p_1(E_{k+1}^{(n)}))^2 + \sum_{i=1}^{k+1} \sum_{j=k+2}^{n} (x_i - p_i(E_{k+1}^{(n)})) \alpha_{ij} x_j$$

$$+ \sum_{i=k+2}^{n} \epsilon_i \beta_i x_i + \sum_{i=k+2}^{n} \sum_{j=1}^{k+1} x_i \alpha_{ij} x_j ,$$

since $[\alpha_{ij}]_{i,j=1,\ldots,k+1}$ and $[\alpha_{ij}]_{i,j=k+2,\ldots,n}$ are

anti-symmetric and

$$p_j(E_{k+1}^{(n)}) = 0 \qquad (k+2 \leq j \leq n) .$$

Now

$$\sum_{i=1}^{k+1} \sum_{j=k+2}^{n} x_i \alpha_{ij} x_j = \sum_{j=1}^{k+1} \sum_{i=k+2}^{n} x_j \alpha_{ji} x_i$$

$$= - \sum_{j=1}^{k+1} \sum_{i=k+2}^{n} x_j \alpha_{ij} x_i , \qquad \text{by the anti-asymmetry of } [\alpha_{ij}]$$

$$= - \sum_{i=k+2}^{n} \sum_{j=1}^{k+1} x_i \alpha_{ij} x_j .$$

Therefore

$$W'(x_1,x_2,\ldots,x_n) = -\lambda_1\beta_1(x_1-p_1(E_{k+1}^{(n)}))^2 - \sum_{i=1}^{k+1} \sum_{j=k+2}^{n} p_i(E_{k+1}^{(n)}) \alpha_{ij} x_j$$

$$+ \sum_{i=k+2}^{n} \epsilon_i \beta_i x_i$$

$$= - \lambda_1 \beta_1 (x_1-p_1(E_{k+1}^{(n)}))^2$$

$$+ \sum_{j=k+2}^{n} [\epsilon_j \beta_j - \sum_{i=1}^{k+1} p_i(E_{k+1}^{(n)}) \alpha_{ij}] x_j .$$

Claim 1:

$$\epsilon_j \beta_j - \sum_{i=1}^{k+1} p_i(E_{k+1}^{(n)}) \alpha_{ij} \leq 0 \qquad (k+2 \leq j \leq n) .$$

Proof: Case 1: $k+2 < j \leq n$. Then $\alpha_{ij} = 0 \quad \forall \ 1 \leq i \leq k+1$

so that

$$\epsilon_j \beta_j - \sum_{i=1}^{k+1} p_i(E_{k+1}^{(n)})\, \alpha_{ij} = \epsilon_j \beta_j < 0$$

(since $\epsilon_j < 0 \quad (2 \le j \le n)$ and $\beta_j > 0 \quad (1 \le j \le n)$).

Case 2: $j = k+2$. Then since $\alpha_{ij} = 0 \quad \forall\ 1 \le i \le k$

$$\epsilon_j \beta_j - \sum_{i=1}^{k+1} p_i(E_{k+1}^{(n)})\, \alpha_{ij}$$

$$= \epsilon_{k+2} \beta_{k+2} - p_{k+1}(E_{k+1}^{(n)})\, \alpha_{k+1\ k+2}$$

$$= - a_{k+2\ 0} \left(1 \frac{a_{12}}{a_{21}} \cdots \frac{a_{k+1\ k+2}}{a_{k+2\ k+1}}\right)$$

$$+ \left(a_{12} \frac{a_{23}}{a_{21}} \cdots \frac{a_{k+1\ k+2}}{a_{k+1\ k}}\right)\left(a_{10} - \sum_{i=1}^{h} a_{2i\ 0} \prod_{j=1}^{i} \frac{a_{2j-2\ 2j-1}}{a_{2j\ 2j-1}} \right.$$

$$\left. - \sum_{i=1}^{h} a_{2i+1\ 0} \prod_{j=1}^{i} \frac{a_{2j-1\ 2j}}{a_{2j+1\ 2j}} \right)$$

where

$$h = \begin{cases} \frac{k}{2} & \text{if } k \text{ is even} \\ \frac{k-1}{2} & \text{if } k \text{ is odd} \end{cases}$$

and

$$a_{2h+1} = 0 \qquad \text{if } h \text{ is even.}$$

(since $p_{k+1}(E_{k+1}^{(n)}) = p_{k+1}(E_{k+1}^{(k+1)}) = \mu^{(k+1)}$ and $\alpha_{k+1\ k+2}$, β_{k+2} are as given in Lemma 4.2.1)

$$= a_{12} \frac{a_{23}}{a_{21}} \cdots \frac{a_{k+1\ k+2}}{a_{k+1\ k}} \cdot$$

$$\cdot \left[- \frac{a_{k+2\ 0}}{a_{k+2\ k+1}} + a_{10} - \sum_{i=1}^{h} a_{2i\ 0} \prod_{j=1}^{i} \frac{a_{2j-2\ 2j-1}}{a_{2j\ 2j-1}} \right.$$

$$\left. - \sum_{i=1}^{h} a_{2i+1\ 0} \prod_{j=1}^{i} \frac{a_{2j-1\ 2j}}{a_{2j+1\ 2j}} \right] .$$

We divide it into two cases.

Subcase 2.1: k is even. Now

$$\mu_n^{(n)} \leq \mu_{k+1}^{(n)} \Longrightarrow \mu^{(k+2)} < 0$$

and

$$\mu^{(k+2)} = \mu^{(2h+2)} = \mu^{2(h+1)}$$

$$= a_{10} - \sum_{i=1}^{h+1} a_{2i\ 0} \prod_{j=1}^{i} \frac{a_{2j-2\ 2j-1}}{a_{2j\ 2j-1}} - \sum_{i=1}^{h} a_{2i+1\ 0} \prod_{j=1}^{i} \frac{a_{2j-1\ 2j}}{a_{2j+1\ 2j}}$$

$$= a_{10} - \frac{a_{k+2\ 0}}{a_{k+2\ k+1}} - \sum_{i=1}^{h} a_{2i\ 0} \prod_{j=1}^{i} \frac{a_{2j-2\ 2j-1}}{a_{2j\ 2j-1}}$$

$$- \sum_{i=1}^{h} a_{2i+1\ 0} \prod_{j=1}^{i} \frac{a_{2j-1\ 2j}}{a_{2j+1\ 2j}} .$$

Therefore

$$\epsilon_j \beta_j - \sum_{i=1}^{k+1} p_i(E_{k+1}^{(n)}) \alpha_{ij} \leq 0 .$$

Subcase 2.2: k is odd. Now

$$\mu^{(n)} \leq \mu_{k+1}^{(n)} \Longrightarrow \mu^{(k+1)} < 0$$

and

$$\mu^{(k+2)} = \mu^{(2(h+1)+1)}$$

$$= a_{10} - \sum_{i=1}^{h+1} a_{2i\,0} \prod_{j=1}^{i} \frac{a_{2j-2\;2j-1}}{a_{2j\;2j-1}} - \sum_{i=1}^{h+1} a_{2i+1\,0} \prod_{j=1}^{i} \frac{a_{2j-1\;2j}}{a_{2j+1\;2j}}$$

$$= a_{10} - \frac{a_{k+2\,0}}{a_{k+2\;k+1}} - a_{k+1\,0} \prod_{j=1}^{h+1} \frac{a_{2j-2\;2j-1}}{a_{2j\;2j-1}}$$

$$- \sum_{i=1}^{h} a_{2i\,0} \prod_{j=1}^{i} \frac{a_{2j-2\;2j-1}}{a_{2j\;2j-1}} - \sum_{i=1}^{h} a_{2i+1\,0} \prod_{j=1}^{i} \frac{a_{2j-1\;2j}}{a_{2j+1\;2j}} .$$

Therefore again

$$\epsilon_j \beta_j - \sum_{i=1}^{k+1} p_i(E_{k+1}^{(n)})\, \alpha_{ij} \leq 0 .$$

Claim 2: (i) $W(E_{k+1}^{(n)}) = 0$ and

$W(x) > 0$ for $x \in B_{k+1}$, $x \neq E_{k+1}^{(n)}$

(ii) $W(x) \to \infty$ as $||x|| \to \infty$ or as x tends to any of the hyperplanes H_i $(1 \leq i \leq k+1)$

(iii) Let $M = \{x \in B_{k+1} : x_1 = p_1(E_{k+1}^{(n)})\}$. Then

$W'(x) < 0$ outside M

and

$W'(x) \leq 0$ on M

(iv) M contains no entire trajectories of (I_n) except $E_{k+1}^{(n)}$.

Proof: (Easy, (c.f., Lemma 2.2.2 and part (i)).

It then follows from Barbashin-Krasovskii's theorem that $E_{k+1}^{(n)}$ attracts every solution of (I_n) with initial condition in B_{k+1} and hence it is globally stable. □

Corollary 4.6.2: If $\mu \leq 0$, then (I_n) is non-persistent.

Proof: (By Theorem 4.6.1.). □

§4.7 Some Perturbation Theorems

In this section, we shall consider two perturbed models of (I_n), one with small autonomous perturbation and the other with small periodic forcing.

Model 1: Consider the following perturbed model of (I_n).

$$(P(\epsilon)) \quad \begin{cases} x_1' = x_1(a_{10} - a_{11}x_1 - a_{12}x_2 + \epsilon f_1(x_1,\ldots,x_n)) \\ x_2' = x_2(-a_{20} + a_{21}x_1 - a_{23}x_3 + \epsilon f_2(x_1,\ldots,x_n)) \\ \cdot \\ \cdot \\ \cdot \\ x_{n-1}' = x_{n-1}(-a_{n-1\,0} + a_{n-1\,n-2}x_{n-2} - a_{n-1\,n}x_n + \epsilon f_{n-1}(x_1,\ldots,x_n)) \\ x_n'' = x_n(-a_{n\,0} + a_{n\,n-1}x_{n-1} + \epsilon f_n(x_1,\ldots,x_n)) \end{cases}$$

where all the specified a_{ij} are > 0, ϵ is a small parameter, and, f_i $(i = 1,\ldots,n)$ are C^1.

We know that if $\mu > 0$ (where μ is defined in §4.3), then $(P(0))$ has a globally asymptotically stable positive equilibrium x^*. The following theorem states that under the assumption $\mu > 0$, then for $\epsilon \neq 0$, an asymptotically stable positive equilibrium point $E(\epsilon)$ of $(P(\epsilon))$ bifurcates from x^*.

Theorem 4.7.1: If $\mu > 0$, then $\exists\ \epsilon_0 > 0$ such that for $|\epsilon| < \epsilon_0$

(i) there exists a continuous function $\epsilon \longmapsto E(\epsilon)$ defined for $|\epsilon| < \epsilon_0$ such that $E(0) = x^*$ and $E(\epsilon)$ is a positive equilibrium point of $(P(\epsilon))$,

(ii) $E(\epsilon)$ (for $|\epsilon| < \epsilon_0$) is asymptotically stable.

Proof: Since the proof is standard, we shall only give a sketch of it. For (i), define the map

$$T(x, \epsilon) = \begin{bmatrix} a_{10} - a_{11}x_1 - a_{12}x_2 + \epsilon f_1(x_1,\ldots,x_n) \\ -a_{20} + a_{21}x_1 - a_{23}x_3 + \epsilon f_2(x_1,\ldots,x_n) \\ \cdot \\ \cdot \\ \cdot \\ -a_{n\,0} + a_{n\,n-1}x_{n-1} + \epsilon f_n(x_1,\ldots,x_n) \end{bmatrix}$$

Then $T(x^*,0) = 0$ and $T'(x^*,0) = M$ is non-singular, where T' is the Jabobian matrix $\left(\frac{\partial T^i}{\partial x_j}\right)$ and M is the variational matrix of (I_n) at x^*.

(i) then follows from the Implicit Function Theorem (see, e.g., Rudin [36], p. 196, Theorem 9.18). For (ii), set $y = x - E(\epsilon)$.

Clearly $(P(0)) = (I_n)$ can be rewritten as

$$y' = My + g(y) \quad .$$

Moreover, in general, $(P(\epsilon))$ can be rewritten as

$$y' = My + g(y) + \epsilon(h(y+E(\epsilon)) - h(E(\epsilon))) + q(y,\epsilon)$$

where

$$h(x) = \begin{bmatrix} x_1 f_1(x) \\ \cdot \\ \cdot \\ \cdot \\ x_n f_n(x) \end{bmatrix}$$

and $q(y,\epsilon) = g(y + E(\epsilon)) - g(y + E(0)) - g(E(\epsilon)) + g(E(0))$. Using the fact that $E(\epsilon)$ is continuous in ϵ, it can be shown that there exists a continuous function $S(\epsilon)$ of ϵ such that

$$S(0) = 0 \quad \text{and} \quad ||q(y,\epsilon)|| \leq ||S(\epsilon)||\,||y|| \ .$$

On the other hand, by the Mean-Value theorem, it can be shown that

$$\forall\, p > 0, \quad \exists\, r_1 = r_1(p), \quad r_2 = r_2(p)$$

such that

$$||y|| \leq p \Longrightarrow ||h(y+E(\epsilon))-h(E(\epsilon))|| \leq r_1||y|| + r_2||E(\epsilon)||\,||y|| \ .$$

Knowing these estimates on h and q, the asymptotic stability of $E(\epsilon)$ follows immediately from the Variation of Constants formula and Gronwall's inequality (c.f., Hale [33], p. 86, Theorem 2.4). □

Model 2: Consider the following perturbed model of (I_n).

$$(Q(\epsilon)) \begin{cases} x_1' = x_1(a_{10} - a_{11}x_1 - a_{12}x_2) + \epsilon\, f_1(x_1,\ldots,x_n,t) \\ x_2' = x_2(-a_{20} + a_{21}x_1 - a_{23}x_3) + \epsilon\, f_2(x_1,\ldots,x_n,t) \\ \cdot \\ \cdot \\ \cdot \\ x_{n-1}' = x_{n-1}(-a_{n-1\,0} + a_{n-1\,n-2}x_{n-2} - a_{n-1\,n}x_n) + \epsilon f_{n-1}(x_1,\ldots,x_n,t) \\ x_n' = x_n(-a_{n\,0} + a_{n\,n-1}x_{n-1}) + \epsilon\, f_n(x_1,\ldots,x_n,t) \end{cases}$$

where all the specified a_{ij} are > 0, ϵ is a small parameter, f_i $(i = 1,\ldots,n)$ are C^1 and periodic in t with period w.

The following theorem states that if $\mu > 0$, then for $\epsilon \neq 0$, an asymptotically stable periodic solution of $(Q(\epsilon))$ of period w bifurcates from the positive equilibrium x^* of $(Q(0))$.

Theorem 4.7.2: If $\mu > 0$, then for small $|\epsilon|$, $(Q(\epsilon))$ has an asymptotically stable solution $x(t,\epsilon)$, periodic in t of period w, continuous in (t,ϵ), and with $x(t,0) = x^*$. Moreover, there is only one such solution for each ϵ.

Proof: The proof follows trivially from Coddington and Levinson [35], p. 348, Theorem 1.1 and p. 350, Theorem 1.2 and the fact that all eigenvalues of M have negative real parts (see Corollary 4.3.3 (ii)).

□

CHAPTER V

EFFECT OF EVOLUTION ON EQUILIBRIUM NUMBERS

§5.1 Introduction

Our purpose in this chapter is to investigate the effect of selection on the abundance of species of a food chain at equilibrium. In particular, we are concerned with the question: "is the driving force of selection within a species generally directed so as to make the species more abundant, or can selection leave equilibrium numbers unaffected or even operate so as to decrease abundance?"

A method which we now briefly describe for this analysis is given in Levins [37].

"Suppose that the dynamics of a community of n variables is given by the set of n differential equations (1.1.1). There may be one or more equilibrium points of the system at which all the f_i's are zero. In the neighborhood of any equilibrium point the behavior of the system depends on the properties of the community matrix

$$M = \begin{bmatrix} m_{11} & m_{12} & \cdots & m_{1n} \\ m_{21} & m_{22} & \cdots & m_{2n} \\ \cdot & & & \\ \cdot & & & \\ \cdot & & & \\ m_{n1} & m_{n2} & \cdots & m_{nn} \end{bmatrix}$$

where the elements m_{ij} are given by

$$m_{ij} = \frac{\partial f_i}{\partial x_j}$$

evaluated at the equilibrium point.

If a genetic variant arises which alters a parameter C_h, it can of course affect many of the species in the system, both directly and indirectly. But it will be selected only if

$$\frac{\partial f_i}{\partial C_h} > 0 \quad .$$

Therefore the action and direction of Mendelian selection is determined by the function f_i for the species in question. But the consequences of that selection depend on the whole ensemble of species and their interrelation, since f_i for one species may depend on all the x_is.

If C_h is a parameter under genetic control of species i (e.g., its bill length, rate of larval development, ability to escape predators, etc.), then C_h will increase under selection when it enters the growth equation

$$x_i' = f_i(x_1, x_2, \ldots, x_n; C_1, C_2, \ldots) \tag{5.1.1}$$

for species i with a positive coefficient, that is $\frac{\partial f_i}{\partial C_h} > 0$. To determine the effect of C_h on the equilibrium levels of all the species in the community, we must differentiate the system of expressions on the right of equation (5.1.1) (one such expression for each species x_i), with respect to C_h, and set the derivatives equal to zero:

$$\sum_{j=1}^{n} \left(\frac{\partial f_i}{\partial x_j}\right)\left(\frac{\partial x_j}{\partial C_h}\right) + \left(\frac{\partial f_i}{\partial C_h}\right) = 0 \qquad (i = 1,2,\ldots,n) \tag{5.1.2}$$

or in matrix form

$$(5.1.3)\qquad \begin{bmatrix} m_{11} & m_{12} & \cdots & m_{1n} \\ m_{21} & m_{22} & \cdots & m_{2n} \\ \cdot & & & \\ \cdot & & & \\ \cdot & & & \\ m_{n1} & m_{n2} & \cdots & m_{nn} \end{bmatrix} \begin{bmatrix} \frac{\partial x_1}{\partial C_h} \\ \frac{\partial x_2}{\partial C_h} \\ \cdot \\ \cdot \\ \cdot \\ \frac{\partial x_n}{\partial C_h} \end{bmatrix} = - \begin{bmatrix} \frac{\partial f_1}{\partial C_h} \\ \frac{\partial f_2}{\partial C_h} \\ \cdot \\ \cdot \\ \cdot \\ \frac{\partial f_n}{\partial C_h} \end{bmatrix}$$

Solving (5.1.3) for the unknown $\frac{\partial x_i}{\partial C_h}$ we have

$$\frac{\partial x_i}{\partial C_h} = \frac{\det \begin{bmatrix} m_{11} & m_{12} & \cdots & -\frac{\partial f_1}{\partial C_h} & \cdots & m_{1n} \\ m_{21} & m_{22} & \cdots & -\frac{\partial f_2}{\partial C_h} & \cdots & m_{2n} \\ \cdot & & & & & \\ \cdot & & & & & \\ \cdot & & & & & \\ m_{n1} & m_{n2} & \cdots & -\frac{\partial f_n}{\partial C_h} & \cdots & m_{nn} \end{bmatrix}}{\det M} \quad (i^{th} \text{ column})$$

In §5.2 and §5.3 we shall consider food chains which have an equilibrium point at which the community matrix M takes the form

$$M = \begin{bmatrix} m_{11} & m_{12} & & & & \\ m_{21} & 0 & m_{23} & & & \\ & m_{32} & 0 & m_{34} & & \\ & \cdot & \cdot & \cdot & \cdots & \\ & \cdot & \cdot & \cdot & \cdots & \\ & \cdot & \cdot & \cdot & \cdots & \\ & & & & m_{n-1\ n-2} & 0 & m_{n-1\ n} \\ & & & & & m_{n\ n-1} & 0 \end{bmatrix}$$

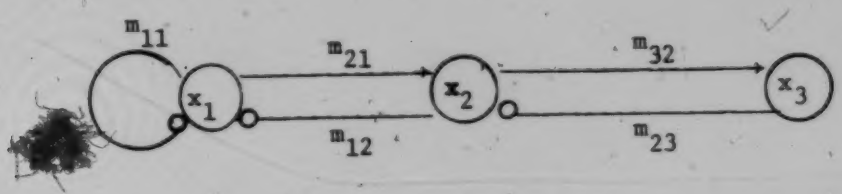
where $m_{11}, m_{12}, m_{23}, \ldots, m_{n-1\ n} < 0$; $m_{21}, m_{32}, \ldots, m_{n\ n-1} > 0$ and all the unspecified entries are zero (c.f., Corollary 2.2.2).

Moreover, we make the simplifying assumption that for each $h = 1,2,\ldots,n$ trait C_h directly affects only the biology of the h^{th} species. Therefore

$$\frac{\partial f_h}{\partial C_h} > 0 \quad \text{and} \quad \frac{\partial f_i}{\partial C_h} = 0 \quad (\text{for } i \neq h) .$$

§5.2 n = 3, 4

(1) n = 3: In the following diagram, we have a three-species hierarchy of plants x_1, herbivore x_2, and a carnivore x_3.



Evolution towards increased overall viability or fecundity can occur in any of the three species. To determine what effect selection in a species will have on its own abundance and that of the other species, we evaluate the following determinants.

Since

$$\det \begin{bmatrix} m_{11} & m_{12} & 0 \\ m_{21} & 0 & m_{23} \\ 0 & m_{32} & 0 \end{bmatrix} = -m_{11}m_{23}m_{32} < 0$$

$$\det \begin{bmatrix} -\frac{\partial f_1}{\partial C_1} & m_{12} & 0 \\ 0 & 0 & m_{23} \\ 0 & m_{32} & 0 \end{bmatrix} = \frac{\partial f_1}{\partial C_1} m_{23}m_{32} < 0$$

$$\det \begin{bmatrix} m_{11} & -\frac{\partial f_1}{\partial C_h} & 0 \\ m_{21} & 0 & m_{23} \\ 0 & 0 & 0 \end{bmatrix} = 0$$

and

$$\det \begin{bmatrix} m_{11} & m_{12} & -\frac{\partial f_1}{\partial C_1} \\ m_{21} & 0 & 0 \\ 0 & m_{32} & 0 \end{bmatrix} = -\frac{\partial f_1}{\partial C_1} m_{21} m_{32} < 0$$

therefore

$$\frac{\partial x_1}{\partial C_1} = \frac{\frac{\partial f_1}{\partial C_1} m_{23} m_{32}}{-m_{11} m_{23} m_{32}} > 0$$

$$\frac{\partial x_2}{\partial C_1} = \frac{0}{-m_{11} m_{23} m_{32}} = 0$$

and

$$\frac{\partial x_3}{\partial C_1} = \frac{-\frac{\partial f_1}{\partial C_1} m_{21} m_{32}}{-m_{11} m_{23} m_{32}} > 0 .$$

Similarly one can verify that

$$\frac{\partial x_1}{\partial C_2} = 0, \quad \frac{\partial x_2}{\partial C_2} = 0, \quad \frac{\partial x_3}{\partial C_2} > 0$$

and

$$\frac{\partial x_1}{\partial C_3} > 0, \quad \frac{\partial x_2}{\partial C_3} < 0, \quad \frac{\partial x_3}{\partial C_3} > 0 .$$

Therefore,

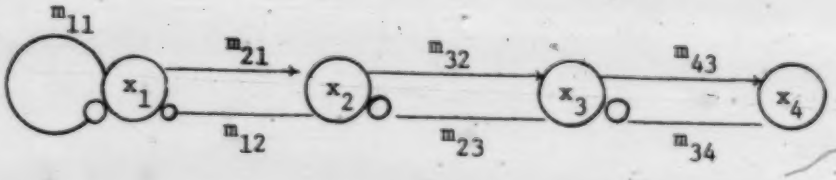
(i) evolution in the plant increases the abundance of the plant,

leaves the abundance of the herbivore unchanged; the herbivore has more food but suffers heavier predation and merely has a higher turnover rate, increasing the abundance of the carnivore;

(ii) evolution in the herbivore (e.g., towards increased efficiency of digestion) does not increase its own population level, and does not affect the plant population, but instead increases the abundance of the carnivore;

(iii) evolution in the carnivore affects all three levels: the plants increase, the herbivores decrease and the carnivores increase.

(2) $\underline{n = 4}$: In the following diagram, we have a four-species hierachy of plants x_1, herbivore x_2, carnivore x_3 and secondary carnivore x_4.



As in the $n = 3$ case, one may easily verify that

$$\frac{\partial x_1}{\partial C_1} = 0, \quad \frac{\partial x_2}{\partial C_1} > 0, \quad \frac{\partial x_3}{\partial C_1} = 0, \quad \frac{\partial x_4}{\partial C_1} > 0$$

$$\frac{\partial x_1}{\partial C_2} < 0, \quad \frac{\partial x_2}{\partial C_2} > 0, \quad \frac{\partial x_3}{\partial C_2} = 0, \quad \frac{\partial x_4}{\partial C_2} > 0$$

$$\frac{\partial x_1}{\partial C_3} = 0, \quad \frac{\partial x_2}{\partial C_3} = 0, \quad \frac{\partial x_3}{\partial C_3} = 0, \quad \frac{\partial x_4}{\partial C_3} > 0$$

and

$$\frac{\partial x_1}{\partial C_4} < 0, \quad \frac{\partial x_2}{\partial C_4} > 0, \quad \frac{\partial x_3}{\partial C_4} < 0, \quad \frac{\partial x_4}{\partial C_4} > 0 \ .$$

Analogous conclusions can then be drawn for this case $(n = 4)$ as in the previous one $(n = 3)$.

Remark. The case $n = 3$ has been considered by Levins [37].

§5.3 General n

Lemma 5.3.1:

$$\det A_n \equiv \det \begin{bmatrix} 0 & m_{12} & & & & & \\ m_{21} & 0 & m_{23} & & & & \\ & m_{32} & \cdot & \cdots & & & \\ & & & \cdots & & & \\ & & & \cdots & & & \\ & & & & \cdot & \cdot & \cdot \\ & & & & & \cdot & m_{n-1\,n} \\ & & & & \cdot & m_{n\,n-1} & 0 \end{bmatrix}$$

$$= \begin{cases} 0, & \text{if } n \text{ is odd} \\ (-1)^k m_{12}m_{21}^{n}{}_{34}m_{43} \cdots m_{n-1\,n}m_{n\,n-1}, & \text{if } n \text{ is even} \\ & (n = 2k, \text{ say}) . \end{cases}$$

Proof: (By induction on n). Clearly it is true for n = 1,2,3,4. Suppose that it is true for n and n+1. We want to show that it is also true for n+2. Now

$$\det A_{n+2} = -m_{12} \det \begin{bmatrix} m_{21} & m_{23} & & & & & \\ 0 & 0 & m_{34} & & & & \\ & m_{43} & \cdot & \cdots & & & \\ & & & \cdots & & & \\ & & & \cdots & & & \\ & & & \cdots & & & \\ & & & & \cdot & \cdot & m_{n+1\,n+2} \\ & & & & \cdot & m_{n+2\,n+1} & 0 \end{bmatrix}$$

$$= -m_{12}m_{21} \det \begin{bmatrix} 0 & m_{34} & & & & & \\ m_{43} & \cdot & \cdots & & & & \\ & & \cdots & & & & \\ & & \cdots & & & & \\ & & \cdots & & & & \\ & & & \cdot & \cdot & \cdot & \\ & & & \cdot & \cdot & m_{n+1\ n+2} & \\ & & & \cdot & m_{n+2\ n+1} & 0 & \end{bmatrix}$$

Case 1: n is odd. Then induction hypothesis gives

$$\det \begin{bmatrix} 0 & m_{34} & & & & & \\ m_{43} & \cdot & & & & & \\ & & \cdots & & & & \\ & & \cdots & & & & \\ & & \cdots & & & & \\ & & & \cdot & \cdot & \cdot & \\ & & & \cdot & \cdot & m_{n+1\ n+2} & \\ & & & \cdot & m_{n+2\ n+1} & 0 & \end{bmatrix} = 0$$

so that $\det A_{n+2} = 0$.

Case 2: n is even, $n = 2k$, say. Then, again by the induction hypothesis

$$\det \begin{bmatrix} 0 & m_{34} & & & & \\ m_{43} & \cdot & & & & \\ & & \cdots & & & \\ & & \cdots & & & \\ & & \cdots & & & \\ & & & \cdot & \cdot & \\ & & & \cdot & m_{n+1\ n+2} & \\ & & & m_{n+2\ n+1} & 0 & \end{bmatrix}$$

$$= (-1)^k \, m_{34} m_{43} m_{56} m_{65} \cdots m_{n+1\ n+2} \, m_{n+2\ n+1} \, .$$

so that

$$\det A_{n+2} = (-1)^{k+1} \, m_{12} m_{21} m_{34} m_{43} \cdots m_{n+1\ n+2} \, m_{n+2\ n+1} \, .$$

□

Remark: If $m_{12}, m_{23}, \ldots, m_{n-1\ n} < 0$ and $m_{21}, m_{32}, \ldots, m_{n\ n-1} > 0$ then

$$\det A_n \begin{cases} = 0 & \text{if } n \text{ is odd} \\ > 0 & \text{if } n \text{ is even} \end{cases}$$

Lemma 5.3.2:

$$\det M = \begin{cases} (-1)^k \, m_{11} m_{23} m_{32} m_{45} m_{54} \cdots m_{n-1\ n} \, m_{n\ n-1} & \text{if } n = 2k+1 \\ & (0 \leq k < \infty) \text{ is odd} \\ (-1)^k \, m_{12} m_{21} m_{34} m_{43} \cdots m_{n-1\ n} \, m_{n\ n-1} & \text{if } n = 2k \\ & (1 \leq k < \infty) \text{ is even.} \end{cases}$$

Proof: It is clearly true for $n = 1,2,3,4$. Now,

$$\det M = \det \begin{bmatrix} m_{11} & m_{12} & & & & & \\ m_{21} & 0 & m_{23} & & & & \\ & m_{12} & \cdot & & & & \\ & & & \cdots & & & \\ & & & \cdots & & & \\ & & & \cdots & & & \\ & & & & \cdot & \cdot & \\ & & & & \cdot & m_{n-1\,n} & \\ & & & & m_{n\,n-1} & 0 & \end{bmatrix}$$

$$= m_{11} \begin{bmatrix} 0 & m_{23} & & & & & \\ m_{32} & \cdot & \cdot & & & & \\ & \cdot & \cdot & & & & \\ & & & \cdots & & & \\ & & & \cdots & & & \\ & & & \cdots & & & \\ & & & & \cdot & \cdot & \\ & & & & \cdot & m_{n-1\,n} & \\ & & & & m_{n\,n-1} & 0 & \end{bmatrix}$$

$$
-m_{12} \det \begin{bmatrix}
m_{21} & m_{23} & & & & \\
0 & 0 & m_{34} & & & \\
 & m_{43} & \cdot & & & \\
 & & \cdots & & & \\
 & & \cdots & & & \\
 & & \cdots & & & \\
 & & & \cdot & \cdot & \cdot \\
 & & & \cdot & \cdot & m_{n-1\,n} \\
 & & & \cdot & m_{n\,n-1} & 0
\end{bmatrix}
$$

$$
= m_{11} \det \begin{bmatrix}
0 & m_{23} & & & & \\
m_{32} & \cdot & & & & \\
 & & \cdots & & & \\
 & & \cdots & & & \\
 & & \cdots & & & \\
 & & & \cdot & \cdot & \cdot \\
 & & & \cdot & \cdot & m_{n-1\,n} \\
 & & & \cdot & m_{n\,n-1} & 0
\end{bmatrix}
$$

$$
- m_{12}\, m_{21} \det \begin{bmatrix}
0 & m_{34} & & & & \\
m_{43} & \cdot & & & & \\
 & & \cdots & & & \\
 & & \cdots & & & \\
 & & \cdots & & & \\
 & & & \cdot & \cdot & \cdot \\
 & & & \cdot & \cdot & m_{n-1\,n} \\
 & & & \cdot & m_{n\,n-1} & 0
\end{bmatrix}
$$

Case 1: $n = 2k+1$ is odd. Then

$$\det M = m_{11}\,(-1)^k\, m_{23}\, m_{32}\, m_{45}\, m_{54} \cdots m_{n-1\,n}\, m_{n\,n-1}\ ,$$

by Lemma 5.3.1.

Case 2: $n = 2k$ is even. Then

$$\det M = -m_{12}\, m_{21}\, (-1)^{k-1}\, m_{34}\, m_{43}\, m_{56}\, m_{65} \cdots m_{n-1\,n}\, m_{n\,n-1}\ ,$$

by Lemma 5.3.1. □

Remark: Since $m_{11}, m_{12}, \ldots, m_{n-1\,n} \leq 0$, and $m_{21}, \ldots, m_{n\,n-1} > 0$, therefore,

$$\det M \begin{cases} < 0 & \text{if } n \text{ is odd} \\ > 0 & \text{if } n \text{ is even} \end{cases}.$$

Let M_j^i be the $n \times n$ matrix obtained from M by replacing the j^{th} column of M by

$$\begin{bmatrix} 0 \\ \vdots \\ 0 \\ -\dfrac{\partial f_i}{\partial c_i} \\ 0 \\ \vdots \\ 0 \end{bmatrix} \leftarrow i^{th} \text{ row}\ .$$

Since

$$\frac{\partial x_i}{\partial C_i} = \frac{\det M_j^i}{\det M}$$

and we know the sign of $\det M$ from Lemma 5.3.2, therefore our remaining task is to find out the sign of $\det M_j^i$.

Lemma 5.3.3: (i) When n is odd

$$\det M_j^1 \begin{cases} < 0 & \text{if } j \text{ is odd} \\ = 0 & \text{if } j \text{ is even} \end{cases}$$

(ii) when n is even

$$\det M_j^1 \begin{cases} = 0 & \text{if } j \text{ is odd} \\ > 0 & \text{if } j \text{ is even} \end{cases}$$

Proof:

$$\det M_1^1 = \det \begin{bmatrix} -\frac{\partial f_1}{\partial C_1} & m_{12} & & & & & \\ 0 & 0 & m_{23} & & & & \\ & m_{32} & \cdot & & & & \\ & & & \cdots & & & \\ & & & \cdots & & & \\ & & & \cdots & & & \\ & & & & \cdot & \cdot & \cdot \\ & & & & \cdot & \cdot & m_{n-1\,n} \\ & & & & \cdot & m_{n\,n-1} & 0 \end{bmatrix}$$

$$= -\frac{\partial f_1}{\partial C_1} \det \begin{bmatrix} 0 & m_{23} & & & & \\ m_{32} & \cdot & \cdot & & & \\ & & \cdots & & & \\ & & \cdots & & & \\ & & \cdots & & & \\ & & & \cdot & \cdot & \cdot \\ & & & \cdot & \cdot & m_{n-n\ n} \\ & & & \cdot\ m_{n\ n-1} & & 0 \end{bmatrix} .$$

By the remark following Lemma 5.3.1, when n is odd, $\det M_1^1 < 0$ and when n is even, $\det M_1^1 = 0$.

$$\det M_2' = \det \begin{bmatrix} m_{11} & -\frac{\partial f_1}{\partial C_1} & & & & & & \\ m_{21} & 0 & m_{23} & & & & & \\ & 0 & 0 & m_{34} & & & & \\ & & m_{43} & \cdot & & & & \\ & & & & \cdots & & & \\ & & & & \cdots & & & \\ & & & & \cdots & & & \\ & & & & & \cdot & \cdot & \cdot \\ & & & & & \cdot & \cdot & m_{n-1\ n} \\ & & & & & \cdot\ m_{n\ n-1} & & 0 \end{bmatrix}$$

$$= \frac{\partial}{\partial C_1^1} \det \begin{bmatrix} m_{21} & m_{23} & & & & & \\ 0 & 0 & m_{34} & & & & \\ & m_{43} & \cdot & \cdots & & & \\ & & & \cdots & & & \\ & & & \cdots & & & \\ & & & & \cdot & \cdot & \cdot \\ & & & & \cdot & \cdot & m_{n-1\,n} \\ & & & & \cdot & m_{n\,n-1} & 0 \end{bmatrix}$$

$$= \frac{\partial f_i}{\partial C_1^1} m_{21} \det \begin{bmatrix} 0 & m_{34} & & & & & \\ m_{43} & \cdot & & & & & \\ & & \cdots & & & & \\ & & \cdots & & & & \\ & & \cdots & & & & \\ & & & & \cdot & \cdot & \\ & & & & \cdot & \cdot & m_{n-1\,n} \\ & & & & \cdot & m_{n\,n-1} & 0 \end{bmatrix}.$$

Again by the remark following Lemma 5.3.1, we have, when n is odd, $\det M_2^1 = 0$ and when n is even, $\det M_2^1 > 0$.

In general,

$$\det M_j^1 = \det \begin{bmatrix} & & &

$$= \frac{\partial f_1}{\partial C_1} \det \begin{bmatrix} m_{21} & 0 & m_{23} & & & & & & \\ & m_{32} & \cdot & & & & & & \\ & & \cdots & & & & & & \\ & & \cdots & & & & & & \\ & & \cdots & & & & & & \\ & & & \cdot & m_{j-2\ j-1} & & & & \\ & & & m_{j-1\ j-2} & 0 & 0 & & & \\ & & & & m_{j\ j-1} & m_{j\ j+1} & & & \\ & & & & 0 & 0 & m_{j+1\ j+2} & & \\ & & & & & m_{j+2\ j+1} & \cdot & & \\ & & & & & & \cdots & & \\ & & & & & & \cdots & & \\ & & & & & & \cdots & & \\ & & & & & & & \cdot & \cdot & \cdot \\ & & & & & & & \cdot & \cdot & m_{n-1\ n} \\ & & & & & & & \cdot & m_{n\ n-1} & 0 \end{bmatrix}$$

$$= (-1)^{\delta} \frac{\partial f_1}{\partial C_1} m_{21} m_{32} \cdots m_{j-1\ j-2}\, m_{j\ j-1} \det \begin{bmatrix} 0 & m_{j+1\ j+2} & \cdot & & & \\ m_{j+2\ j+1} & \cdot & \cdot & & & \\ \cdot & \cdot & \cdot & \cdots & & \\ & & & \cdots & & \\ & & & \cdots & & \\ & & & & \cdot & \cdot & \cdot \\ & & & & \cdot & \cdot & m_{n-1\ n} \\ & & & & \cdot & m_{n\ n-1} & 0 \end{bmatrix}$$

where

$$\delta = \begin{cases} 1 & \text{if } j \text{ is odd} \\ 0 & \text{if } j \text{ is even} \end{cases}$$

It follows from the remark following Lemma 5.3.1 that

(i) when n is odd, $\det M_j^1 \begin{cases} < 0 & \text{if } j \text{ is odd} \\ = 0 & \text{if } j \text{ is even} \end{cases}$

(ii) when n is even, $\det M_j^1 \begin{cases} = 0 & \text{if } j \text{ is odd} \\ > 0 & \text{if } j \text{ is even} \end{cases}$.

□

Theorem 5.3.4: (i) when n is odd

$$\frac{\partial x_j}{\partial C_1} \begin{cases} > 0 & \text{if } j \text{ is odd} \\ = 0 & \text{if } j \text{ is even} \end{cases},$$

(ii) when n is even

$$\frac{\partial x_j}{\partial C_1} \begin{cases} = 0 & \text{if } j \text{ is odd} \\ > 0 & \text{if } j \text{ is even} \end{cases}$$

Proof: It follows immediately from Lemma 5.3.2 and Lemma 5.3.3. □

Remark: By expanding $\det M_j^i$ via $\frac{\partial f_i}{\partial C_i}$, it is clear that the procedure described in the proof of Lemma 5.3.3 is equally applicable to calculate the sign of any $\det M_j^i$ $(i,j = 1,2,\ldots,n)$. For example, one can easily show that evolution of the top predator affects the

abundance of all levels in a manner similar to the cases $n = 3,4$. In fact it is not difficult to show that the follwing tables hold:

n = odd

selection of \ effect on abundance of	x_1	x_2	x_3	x_4	x_5	...	x_{n-1}	x_n
x_1	↑	0	↑	0	↑	...	0	↑
x_2	0	0	↓	0	↓	...	0	↓
x_3	↑	↓	↑	0	↑	...	0	↑
x_4	0	0	0	0	↓	...	0	↓
x_5	↑	↓	↑	↓	↑	...	0	↑
.	.	.	.	.	.	...	.	.
.	.	.	.	.	.	...	.	.
.	.	.	.	.	.	...	.	.
x_{n-1}	0	0	0	0	0	...	0	↓
x_n	↑	↓	↑	↓	↑	...	↓	↑

n = even

selection of \ effect on abundance of	x_1	x_2	x_3	x_4	x_5	x_6	...	x_n	x_{n-1}
x_1	0	↑	0	↓	0	↑	...	0	↑
x_2	↓	↑	↓	↑	↓	↑	...	↑	↑
x_3	0	0	0	↑	0	↑	...	0	↑
x_4	↓	↑	↓	↑	↓	↑	...	↓	↑
x_5	0	0	0	0	0	↑	...	0	↑
x_6	↓	↑	↓	↑	↓	↑	...	↓	↑
. . .	. . .	. . .	. . .	. . .	. . .	. . .	... ...	. . .	. . .
x_{n-1}	0	0	0	0	0	0	...	0	↑
x_n	↓	↑	↓	↑	↓	↑	...	↓	↑

where

	x_j	
x_i	+, +, 0	

indicates that selection at the x_i species will increase, decrease or does not change the abundance of the x_j species, respectively.

CHAPTER VI

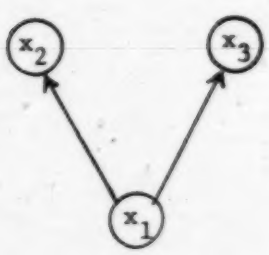
EXAMPLES

One aspect of community ecology that has attracted much attention is the relation between the complexity of a food web and its stability. Here increased 'complexity' means more species, more interaction and hence more parameters characterising the interaction; and, 'stability' means relatively lower levels of population fluctuation, or the ability to recover from perturbation, or simply with persistence of the system. Evidence that such a relationship exists abound. For example, in the study of a marine rocky intertidal community (mussels, barnacles and starfish), Paine [23] showed that predators, Pisaster ochraceus and Thais emarginata, played the major role in maintaining the diversity of prey species. By removing Pisaster, the number of species in the marine rocky intertidal community decreased from 15 to 8 species. However, the issue of whether complexity will promote stability is unclear. For example, Elton [38] has drawn together a collection of empirical and theoretical observations in support of the conclusion that complexity implies stability; whereas, Watt [39] gives examples of simple natural systems that are stable and of complex ones that are not. For a more complete account of the situation and other references, see May [15].

Our purpose in this chapter is to illustrate the model possibility of this question by using Lotka-Volterra ecosystem models with 3 and 4 species.

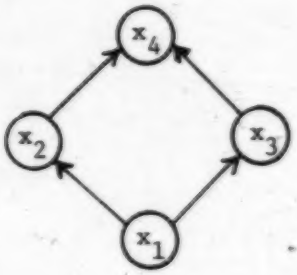
§6.1 Example 1

In this example, we compare the stability of the following two ecocommunities:



(A)

and



(B)

In (A), both predators x_2 and x_3 share the same prey x_1. (B) is the same as (A) except that there is a third predator x_4 feeding on both x_2 and x_3. Suppose (A) and (B) are governed by Lotka-Volterra dynamics, then (A) and (B) can be respectively described by the systems of differential equations (6.1.1) and (6.1.2):

$$(6.1.1)\qquad \begin{cases} x_1' = x_1(a_{10} - a_{11}x_1 - a_{12}x_2 - a_{13}x_3) \\ x_2' = x_2(-a_{20} + a_{21}x_1) \\ x_3' = x_3(-a_{30} + a_{31}x_1) \end{cases}$$

$$(6.1.2)\qquad \begin{cases} x_1' = x_1(a_{10} - a_{11}x_1 - a_{12}x_2 - a_{13}x_3) \\ x_2' = x_2(-a_{20} + a_{21}x_1 - a_{24}x_4) \\ x_3' = x_3(-a_{30} + a_{31}x_1 - a_{34}x_4) \\ x_4' = x_4(-a_{40} + a_{42}x_2 + a_{43}x_3) \end{cases}$$

where all the specified a_{ij} are > 0.

Clearly (6.1.1) will have a positive equilibrium only if

$$\frac{a_{20}}{a_{21}} = \frac{a_{30}}{a_{31}} \quad .$$

It is known that (see, for example, McGehee and Armstrong [17]) extinction occurs for (6.1.1), i.e., for any choice of a_{ij}, there is no asymptotically stable attractor of (6.1.1) in Int (R^n_+). We now show that the addition of predator x_4 has a stabilizing effect, in the sense that there is a range of values of the a_{ij}'s (in fact this set is a cone containing a non-empty open set of the parameter space

$$P = \left\{ A = \begin{bmatrix} a_{10} & a_{11} & a_{12} & a_{13} & 0 \\ a_{20} & a_{21} & 0 & 0 & a_{24} \\ a_{30} & a_{31} & 0 & 0 & a_{34} \\ a_{40} & 0 & a_{42} & a_{43} & 0 \end{bmatrix} : a_{ij} > 0 \right\})$$

such that (6.1.2) has an asymptotically stable positive equilibrium.

Using the Routh-Hurwicz criterion and with the help of the computer, it can be shown that for

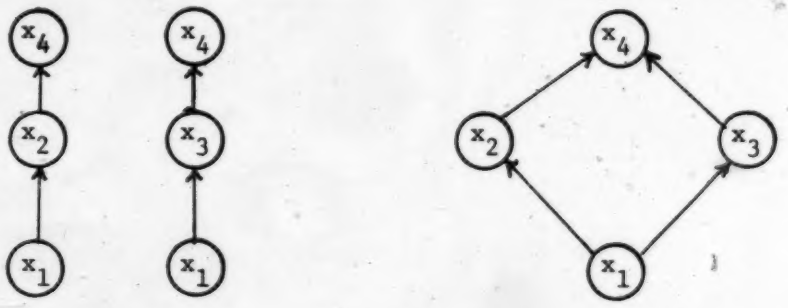
$$(6.1.3) \qquad A = \begin{bmatrix} 2 & 1 & 3 & 4 & 0 \\ 5 & 6 & 0 & 0 & 7 \\ 8 & 9 & 0 & 0 & 5 \\ 1 & 0 & 3 & 1 & 0 \end{bmatrix} .$$

(6.1.2) will have an asymptotically stable positive equilibrium.

The fact that the set of A's for which (6.1.2) has an asymptotically stable positive equilibrium is a cone which contains a non-empty open set then follows.

§6.2 Example 2

In this example, we compare the stability of the following three ecocommunities:



(C) (D) (B)

where (C), (D) and (B) are described by (6.2.1), (6.2.2) and (6.1.2) respectively:

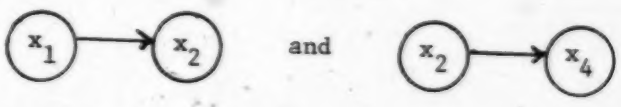
$$(6.2.1)\quad \begin{cases} x_1' = x_1(a_{10} - a_{11}x_1 - a_{12}x_2) \\ x_2' = x_2(-a_{20} + a_{21}x_1 - a_{24}x_4) \\ x_4' = x_4(-a_{40} + a_{42}x_2) \end{cases}$$

$$(6.2.2)\quad \begin{cases} x_1' = x_1(a_{10} - a_{11}x_1 - a_{13}x_3) \\ x_3' = x_3(-a_{30} + a_{31}x_1 - a_{34}x_4) \\ x_4' = x_4(-a_{40} + a_{43}x_3) \end{cases}$$

Let

$$A = \begin{bmatrix} a_{10} & a_{11} & a_{12} & a_{13} & 0 \\ a_{20} & a_{21} & 0 & 0 & a_{24} \\ a_{30} & a_{31} & 0 & 0 & a_{34} \\ a_{40} & 0 & a_{42} & a_{43} & 0 \end{bmatrix}$$

By Theorem 4.6.1, the Routh-Hurwicz criterion and with the help of the computer, it can be shown that for the appropriate restriction of A given in (6.1.3) (D) is non-persistent whereas there is an asymptotically stable positive equilibrium for (B). This indicates that addition of the species x_2 and the two links



to (D) has a stabilizing effect.

However, this is not conclusive because

(i) for

$$A = \begin{bmatrix} 2 & 1 & 3 & 4 & 0 \\ 5 & 6 & 0 & 0 & 7 \\ 8 & 9 & 0 & 0 & 5 \\ 1 & 0 & 3 & 7 & 0 \end{bmatrix}$$

both (C) and (D) survive, but there is no positive equilibrium for (B) and

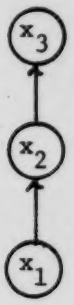
(ii) for

$$A = \begin{bmatrix} 2 & 1 & 1 & 0.1 & 0 \\ 0.9 & 1 & 0 & 0 & 1 \\ 1 & 1 & 0 & 0 & 0.9 \\ 0.1 & 0 & 0.9 & 1 & 0 \end{bmatrix}$$

both (C) and (D) survive and there is an unstable positive equilibrium for (B).

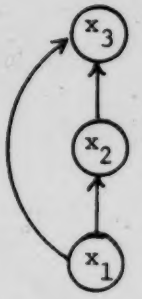
§6.3 Example 3

In this example, we compare the stability of the following two ecocommunities:



(E)

and



(F)

whose dynamics are respectively described by:

$$(6.3.1)\qquad \begin{cases} x_1' = x_1(a_{10} - a_{11}x_1 - a_{12}x_2) \\ x_2' = x_2(-a_{20} + a_{21}x_1 - a_{23}x_3) \\ x_3' = x_3(-a_{30} + a_{32}x_2) \end{cases}$$

$$(6.3.2)\qquad \begin{cases} x_1' = x_1(a_{10} - a_{11}x_1 - a_{12}x_2 - a_{13}x_3) \\ x_2' = x_2(-a_{20} + a_{21}x_1 - a_{23}x_3) \\ x_3' = x_3(-a_{30} + a_{31}x_1 + a_{32}x_2) \end{cases}$$

Our purpose is to see what happens to the stability of the simple food chain (E) (regarding x_1 as plant, x_2 as herbivore and x_3 as carnivore) if the carnivore x_3 becomes an omnivore.

Let

$$A = \begin{bmatrix} a_{10} & a_{11} & a_{12} & a_{13} \\ a_{20} & a_{21} & 0 & a_{23} \\ a_{30} & a_{31} & a_{32} & 0 \end{bmatrix}$$

Using Theorem 4.6.1, the Routh-Hurwicz criterion and with the help of the computer, it can be shown that

(i) for

$$A = \begin{bmatrix} 10 & 1 & 6 & 2 \\ 1 & 5 & 0 & 0.5 \\ 1 & 1 & 1 & 0 \end{bmatrix}$$

(E) survives and there is an asymptotically stable positive equilibrium for (F),

(ii) for

$$A = \begin{bmatrix} 10 & 1 & 4 & 2 \\ 1 & 3 & 0 & 0.5 \\ 1 & 1 & 1 & 0 \end{bmatrix}$$

(E) survives but there is no positive equilibrium for (F),

(iii) for

$$A = \begin{bmatrix} 10 & 1 & 6 & 5 \\ 1 & 5 & 0 & 0.5 \\ 1 & 1 & 1 & 0 \end{bmatrix}$$

(E) survives and there is an unstable positive equilibrium for (F), and,

(iv) for

$$A = \begin{bmatrix} 10 & 1 & 6 & 2 \\ 1 & 5 & 0 & 0.5 \\ 1.7 & 1 & 1 & 0 \end{bmatrix}$$

(E) is non-persistent but there is an asymptotically stable positive equilibrium for (F).

Hence we see that depending on the values of the parameters a_{ij}, all possibilities can occur.

CHAPTER VII

SUMMARY AND DISCUSSION

In Chapter I, we proposed a framework (see §1.1) which is adequate for the investigation of the dynamics of general food webs. The advantage of it is that we can change some of the parameters $C_1, C_2, \ldots$ and see what effect they have on the configuration space. For example, this allows us to study the effect of harvesting, enrichment, migration or evolution on the ecosystem. Mathematical theorems (see §1.2 (1) - (6)) that are useful in the latter chapters are also given.

In Chapter II, ecologically reasonable assumptions (see §2.1 (i) - (vii) and (1) - (8)) are given so that system (1.1.2) represents a straight predator-prey food chain with one species occupying each trophic level. Even though these assumptions are not satisfied by every food chain model studied in literature, they give some indication on the adequacy of a model in simulating the dynamics of a food chain. Theorem 2.2.1 and its Corollary give conditions under which the positive equilibrium of a food chain will be asymptotically stable and for which the variational matrix of (1.1.2) at the equilibrium is qualitatively stable. It is to be noted that these results are quite general (the conditions only impose restrictions on the signs of the entries of the variational matrix and not explicitly on the growth functions $f_1, f_2, \ldots, f_n$ in (1.1.2)). Their applications can be found in Chapters III and IV. Theorem 2.3.1 is a sufficiency theorem on the persistence, non-persistence and survivability of general

food webs. Its usefulness depends on the discovery of a persistent, extinction or survival function. An application of the theorem to Lotka-Volterra food chains, though not given in the above chapters, can be found (at least for parts (i) and (ii) of the theorem) in Gard and Hallam [3]. There is hope that we can use part (iii) of the theorem to improve some persistence results to survivability and that the whole theorem is applicable to more general (other than Lotka-Volterra food chains) situations, such as food chains with Holling types of predation or food webs in general.

Chapter III deals with intermediate food chains (3.1.1). Theorem 3.1.1 states that every solution of an intermediate food chain with a carrying capacity in the first species is bounded. A point to be noted here is that the method of proof of Theorem 3.1.1 is equally applicable to show the boundedness of solutions of a variety of other intermediate type food web models (not necessarily food chains). In §3.2, the conditions are worked out for the existence, uniqueness, asymptotic stability and instability of the equilibrium points of intermediate food chains of length four. Admittedly, the conditions obtained (best possible using linearization) are long (hence uninterst-ing), nevertheless, the procedure of obtaining them well illustrates the use of Routh-Hurwicz criterion, Schwarz matrix theorem and qualitative stability matrix criterion (see §1.2 (2), (3), (4)) in model ecosystem stability considerations.

In Chapter IV, we discuss Lotka-Volterra food chains (4.1.1). By means of Lemma 4.2.1, system (4.1.1) can be rewritten in a form (see (4.2.1)) for which the usual Volterra auxillary function (see the V function in Lemma 4.2.2) can be constructed. Using this Liapunov

function, and under the assumption $a_{11}, a_{22}, \ldots, a_{nn} > 0$, global stability for the positive equilibrium of (4.1.1), if it exists, can be easily proved (see Theorem 4.2.4). In a sense, the validity of this theorem is due to the 'damping' terms $a_{11}, a_{22}, \ldots, a_{nn} > 0$. However, we show in §4.6 that we do not require that much; $a_{11} > 0$ is sufficient to ensure the global stability of the positive equilibrium of (4.1.1). In §4.3 - §4.6, we concentrate on Lotka-Volterra food chains such that $a_{22} = \ldots = a_{nn} = 0$ (see (4.3.1)). The results can be summarized in the following table:

(i) (4.3.1) with $a_{11} > 0$	$\mu > 0$ iff positive equilibrium exists (which is automatically globally stable) ⟹ survivability $\mu < 0$ ⟹ non-persistence
(ii) (4.3.1) with $a_{11} = 0$, n is even	$\mu > 0$ iff positive equilibrium exists (which is automatically stable) ⟹ survivability $\mu < 0$ ⟹ non-persistence
(iii) (4.3.1) with $a_{11} = 0$, n is odd	$\mu > 0$ ⟹ persistence $\mu < 0$ ⟹ non-persistence

For (ii), we also show that each hypersurface V_c $(c \geq 0)$ (see §4.3) contains a recurrent motion. In the case $n = 2$, it is well-known (see Freedman and Waltman [40], for example) that each V_c is in fact a periodic orbit. Therefore, the following questions arise naturally:

(a) does V_c contain any periodic orbit in general?

and

(b) if so, will each solution of (ii) be periodic (except the positive equilibrium itself, of course)?

For (iii), we know that in general there is no positive equilibrium, and that positive equilibria exist when and only when $\mu_0 = 0$. In that case, there will be a half line of equilibria of (iii) in Int (R^n_+) initiating from a point in

$$\{x \in R^n_+ : x_i > 0 \quad (i = 1,\ldots,n-1), \quad x_n = 0\} .$$

Some obvious questions arise:

(a) can we improve persistence, in case $\mu_0 > 0$, to survivability?

and

(b) what happens to the case $\mu_0 = 0$; will the system persist?

For (a), there is hope that Theorem 2.3.1 (iii) is applicable. For (b), Freedman and Waltman [6] show that when $n = 3$ and $\mu_0 = 0$, then every solution of (iii) with initial condition $\in$ Int (R^n_+) is periodic. Therefore we can also ask whether this is true for general n.

So much for (ii) and (iii). For (i), we have a much complete picture (see §4.4 and §4.6). For geometric simplicity, even though it holds for general n, we shall only describe our result for the case $n = 3$ here. Consider the Lotka-Volterra food chain with

three species:

$$\begin{cases} x_1' = x_1(a_{10} - a_{11}x_1 - a_{12}x_2) \\ x_2' = x_2(-a_{20} + a_{21}x_1 - a_{23}x_3) \\ x_3' = x_3(-a_{30} + a_{32}x_2) \end{cases} .$$

There are only four possible equilibria:

$$E_0^{(3)} = (0,0,0), \quad E_1^{(3)} = (\frac{a_{10}}{a_{11}}, 0,0), \quad E_2^{(3)} \quad \text{and} \quad E_3^{(3)}$$

where $E_2^{(3)}$ lies in $\{(x_1,x_2,x_3) \in R^3 : x_1,x_2 > 0 \quad \text{and} \quad x_3 = 0\}$ and $E_3^{(3)}$ is the positive equilibrium, i.e., it lies on

$$\text{Int } (R_+^n) = \{(x_1,x_2,x_3) \in R^3 : x_1,x_2,x_3 > 0\} .$$

$E_0^{(3)}$, $E_1^{(3)}$ always exist whereas the existence of $E_2^{(3)}$ and $E_3^{(3)}$ dependson a parameter $\mu^{(3)}$. In Theorem 4.4.1, we show that there exist numbers $\overline{\mu_1^{(3)}} < 0$ and $\overline{\mu_2^{(3)}} = 0$ such that

$$\overline{\mu_2^{(3)}} < \mu^{(3)} \Longrightarrow E_0^{(3)}, E_1^{(3)}, E_2^{(3)} \text{ and } E_3^{(3)} \text{ all exist}$$

$$\overline{\mu_1^{(3)}} < \mu^{(3)} \leq \overline{\mu_2^{(3)}} \Longrightarrow E_0^{(3)}, E_1^{(3)}, E_2^{(3)} \text{ exist but not } E_3^{(3)}$$

$$\mu^{(3)} \leq \overline{\mu_1^{(3)}} \Longrightarrow E_0^{(3)}, E_1^{(3)} \text{ exist but not } E_2^{(3)} \text{ and } E_3^{(3)} .$$

Note that when $\mu^{(3)} = \overline{\mu_2^{(3)}}$, $E_3^{(3)}$ actually coincides with $E_2^{(3)}$; and when $\mu^{(3)} = \overline{\mu_1^{(3)}}$, $E_2^{(3)}$ coincides with $E_1^{(3)}$. By Theorem 4.6.1,

we know that

$\overline{\mu_2^{(3)}} < \mu^{(3)} \Longrightarrow E_3^{(3)}$ is globally stable over

$\{(x_1,x_2,x_3) : x_1, x_2, x_3 > 0\}$

$E_2^{(3)}$ is globally stable over

$\{(x_1,x_2,x_3) : x_1, x_2 > 0 \text{ and } x_3 = 0\}$

and

$E_1^{(3)}$ is globally stable over

$\{(x_1,x_2,x_3) : x_1 > 0, \ x_2 = x_3 = 0\}$

$\overline{\mu_1^{(3)}} < \mu^{(3)} \leq \overline{\mu_2^{(3)}} \Longrightarrow E_2^{(3)}$ is globally stable over

$\{(x_1,x_2,x_3) : x_1, x_2 > 0, \ x_3 \geq 0\}$

and

$E_1^{(3)}$ is globally stable over

$\{(x_1,x_2,x_3) : x_1 > 0, x_2 = x_3 = 0\}$

and,

$\mu^{(3)} \leq \overline{\mu_1^{(3)}} \Longrightarrow E_1^{(3)}$ is globally stable over

$\{(x_1,x_2,x_3) : x_1 > 0, \ x_2, x_3 \geq 0\}$.

As a consequence, there cannot be any limit cycles in the x_1-x_2 plane nor can there be any non-trivial three dimensional limit sets.

This then answers a question raised by Freedman and Waltman [6].

In §4.5, we show that introduction of a new top predator into an ecosystem would result in an order interchange of equilibrium populations on an alternating scheme. For example, in an aquatic system with trophic levels composed of phytoplankton, herbivores and primary carnivores, the model conclusion predicts that the addition of a secondary carnivore reduces the equilibrium levels of the phytoplankton and primary carnivore while increasing the herbivore population. The two perturbed models $(P(\epsilon))$ and $(Q(\epsilon))$ discussed in §4.7 belong to the non-critical case of perturbation theory (since $\mu > 0$ implies all eigenvalues of the variational matrix of the unperturbed model (I_n) evaluated at the positive equilibrium have negative real parts). Therefore standard theorems apply. A (mathematically) more interesting problem would be to investigate the perturbed models $(P(\epsilon))$ and $(Q(\epsilon))$ when $a_{11} = 0$. Another interesting question is whether the perturbed equilibrium $E(\epsilon)$ in $(P(\epsilon))$ (we know that it is asymptotically stable) is globally stable or not.

Chapter V is an attempt to investigate what effect does selection at each species has on its own abundance and on that of the other species in a food chain. Details for food chains of length three and four are given in §5.2. The results indicate that

(i) Mendelian selection of a species in a food chain may or may not increase the abundance of that species, and,

(ii) the effect of selection on the equilibrium numbers depends on the parity (even or odd) of the length of the food chain.

In Chapter VI, we give some examples to illustrate the model

possibility of the widely discussed topic 'stability verses complexity'. The numerical results that we have obtained tend to indicate that stability of an ecosystem does not simply depend on the number of species present and the number of links between them. Two other important factors are:

(i) the way the species are linked

and

(ii) the relative strength of the links.

However, these examples should not be taken too seriously because

(i) we have assumed that the addition of extra species or extra links does not affect the strength of the original links

and,

(ii) our choice of the values for the parameters a_{ij} has no connection with reality.

BIBLIOGRAPHY

[1] Rescigno, A. and Jones, K.G. (1972), The Struggle for Life: III. A Predator-Prey Chain (Bull. Math. Biophy. 34, 521-532).

[2] Saunders, P.T. and Bazin, M.J. (1975), On the Stability of Food Chains (J. Theo. Bio. 52, 121-142).

[3] Gard, T.C. and Hallam, T.G. (1978), Persistence in Food Webs: I. Lotka-Volterra Food Chains (preprint).

[4] Rosenzweig, M.L. (1973), Exploitation in Three Trophic Levels (Am. Nat. 107, 275-294).

[5] Wollkind, D.J. (1976), Exploitation in Three Trophic Levels: An Extension Allowing Intraspecies Canivore Interaction (Am. Nat. 110, 431-447).

[6] Freedman, H.I. and Waltman, P. (1977), Mathematical Analysis of Some Three-Species Food-Chain Models (Math. Biosc. 33, 257-276).

[7] Hausrath, A.R. (1975), Stability Properties of a Class of Differential Equations Modelling Predator-Prey Relationships (Math. Biosc. 26, 267-281).

[8] Lin, J. and Kahn, P.B. (1978), Qualitative Dynamics of Three-Species Predator-Prey Systems (J. Math. Bio. 5, 257-268).

[9] May, R.M. (1973), Mass and Energy Flow in Closed Ecosystems: A Comment (J. Theo. Bio 39, 155-163).

[10] Hirata, H. and Fukao, T. (1977), A Model of Mass and Energy Flow in Ecosystems (Math. Biosc. 33, 321-334).

[11] Levins, R. (1974), The Qualitative Analysis of Partially Specified Systems (Ann. N.Y. Acad. Sci. 231, 123-138).

[12] Smith, J.M. (1974), Models of Ecology (Cambridge University Press).

[13] Coppel, W.A. (1965), Stability and Asymptotic Behavior of Differential Equations (Health Mathematical Monographs).

[14] Bhatia, N.P. and Szego, G.P. (1967), Dynamical Systems: Stability Theory and Applications (Lecture Notes in Mathematics 35).

[15] May, R.M. (1974), Stability and Complexity in Model Ecosystems (2nd Edition), (Princeton University Press).

[16] Lewontin, R.C. (1969), The Meaning of Stability (Diversity and Stability in Ecological Systems - Brookhaven Symposia in Biology 22).

[17] McGehee, R. and Armstrong, R.A. (1977), Some Mathematical Problems Concerning the Ecological Role of Competitive Exclusion (J. Diff. Eq. 23, 30-52).

[18] Andronov, A.A., Leontovich, E.A., Gordon, I.I., Maier, A.G. (1973), Qualitative Theory of Second-Order Dynamic Systems (John Wiley and Sons) (English Translation).

[19] Schwarz, H.R. (1956), Ein Verfahren zur Stabililitätsfrage bei Matrizen-Eigenwertproblemen (Z. Angew. Math. Phys. 7, 473-500).

[20] Quirk, J.P. and Ruppert, R. (1965), Qualitative Economics and the Stability of Equilibrium (Rev. Econ. Studies 32, 311-326).

[21] Barbashin, E.A. and Krasovskii, N.N. (1952), Stability on the Whole (Dokl. Acad. Nauk SSSR 86, 453-456).

[22] Barbashin, E.A. (1970), Introduction to the Theory of Stability (Wolters-Noordhoff Publishing) (English Translation).

[23] Paine, R.T. (1966), Food Web Complexity and Species Diversity (Am. Nat. 100, 65-75).

[24] Holden, C. (1977), Endangered Species: Review of Law Triggered by Tellico Impasse (Science 196, 1426-1428).

[25] Freedman, H.I. (1976), Graphical Stability, Enrichment, and Pest Control by a Natural Enemy (Math. Biosc. 31, 207-225).

[26] Volterra, V. (1931), Lecons sur la Théorie Mathematique de la Lutte pour la Vie (Gauthier-Villars).

[27] Lotka, A.J. (1925), Elements of Physical Biology (Williams and Wilkins).

[28] D'Ancona, U. (1954), The Struggle for Existence (Brill).

[29] Kerner, E.H. (1969), Gibbs Ensemble and Biological Ensemble (Towards a Theoretical Biology 2).

[30] Goel, N.S., Maitra, S.C. and Montroll, E.W. (1971), On the Volterra and Other Nonlinear Models of Interacting Populations (Rev. Mod. Phys. 43, 231-276).

[31] Rescigno, A. and Richardson, I.W. (1973), The Deterministic Theory of Population Dynamics (Foundations of Mathematical Biology 3).

[32] Goh, B.S. (1977), Global Stability in Many Species Systems (Am. Nat. 111, 135-143).

[33] Hale, J.K. (1969), Ordinary Differential Equations (Wiley-Interscience).

[34] Nemytskii, V.V. and Stepanov, V.V. (1960), Qualitative Theory of Differential Equations (Princeton University Press) (English Translation).

[35] Coddington, E.A. and Levinson, N. (1955), Theory of Ordinary Differential Equations (McGraw-Hill).

[36] Rudin, W. (1964), Principles of Mathematical Analysis (McGraw Hill).

[37] Levins, R. (1975), Evolution in Communities Near Equilibrium (Ecology and Evolution of Communities).

[38] Elton, C.S. (1958), The Ecology of Invasion by Animals and Plants (Methuen and Company).

[39] Watt, K.E.F. (1968), Ecology and Resource Management (McGraw-Hill).

[40] Freedman, H.I. and Waltman, P. (1975), Perturbation of Two-Dimensional Predator-Prey Equations (SIAM J. Appl. Math. 28, 1-10).

[41] Barnett, S. and Storey, C. (1970), Matrix Methods in Stability Theory (Nelson and Sons).